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Research Article

Diversity and host plant utilization of leaf-mining beetles of Chrysomeloidea (Coleoptera) in Japan

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Abstract

The superfamily Chrysomeloidea (Cerambycidae + Chrysomelidae + Megalopodidae) encompasses a diverse phytophagous beetles, whose larvae exhibit internal or external feeding on leaves, wood, or roots of many plants. Through extensive research on leaf-mining insects in Japan, 64 species of Chrysomeloidea were confirmed to engage in leaf-mining behavior during their larval stages infesting tracheophytes, and comprising 2 Cerambycidae, 9 Megalopodidae, and 53 Chrysomelidae. This study presents an overview of the host plants and mining patterns of these 64 leaf-mining beetle species and describes two new species, *Sphaeroderma komiana* Kato, **sp. nov.** and *Dactylispa adinae* Kato, **sp. nov.** The leaf-mining beetles demonstrate a broad host range including Equisetales, Polypodiales, Cycadales, and 23 orders of angiosperms. Particularly notable diversification was observed on Polypodiales (within *Halticorcus*), Ranunculaceae (*Argopus* and *Sphaeroderma*), Celastraceae (*Zeugophora*), and Oleaceae (*Argopistes*). Host specificity greatly varied among the reported 64 beetle species: 29 spp. species-specific; 12 spp. genus-specific; 16 spp. family-specific; 2 spp. order-specific; 5 spp. non-specific even at order level. The five non-specific species (*Argopus punctipennis*, *Sphaeroderma nigricolle*, *Dactylispa angulosa*, *Notosacantha ihai*, and *N. loochooana*) are associated with multiple plant orders while maintaining specificity to a small number of genera belonging to phylogenetically distant plant families. This pattern, termed as extended host specificity, suggests recent host shifts across plant families without substantial expansion of host ranges.

Key words: Cerambycidae, Chrysomelidae, host specificity, leaf miner, Megalopodidae, mining pattern

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Introduction

Leaf mining refers to the lifestyle of phytophagous insect larvae that live, feed, and develop within the internal tissues of plant leaves. This behavior occurs in four holometabolous insect orders: Coleoptera, Hymenoptera, Diptera, and Lepidoptera (Hering 1951). The earliest credible fossil records of leaf mines date back to the Late Triassic period (Imada et al. 2022) and even to the Late Carboniferous period (Knecht et al. 2023). Leaf-mining insects typically exhibit

dorso-ventrally flattened bodies and well-developed mouthparts adaptations for living within the confined spaces of leaves and consuming fibrous plant tissues (Hering 1951). While the plant tissue offers internal leaf miners protection from insect and vertebrate predators, as well as environmental stress, these larvae are still vulnerable to parasitoid attacks. This ecological niche has been adopted by diverse insect leaf-miners.

Leaf-mining species are represented in several coleopteran families, including the Buprestidae, Nitidulidae, Mordellidae, Megalopodidae, Chrysomelidae, Attelabiidae, Brachyceridae, and Curculionidae (Hering 1951; Tooker and Giron 2020; Eiseman 2022). The latter five are part of the clade Phytophaga, which spans two superfamilies, Chrysomeloidea and Curculionoidea, and evolved from the fungus-feeding beetle superfamily Cucujoidea (Hunt et al. 2007; Zhang et al. 2018-. These superfamilies, comprising 59,000 and 53,000 species, respectively, have diversified enormously as angiosperm plants radiated since the Cretaceous period (Farrell 1998; Hunt et al. 2007). The Chrysomeloidea comprises three families: Cerambycidae, Megalopodidae, and Chrysomelidae. Cerambycids are typically wood or shoot borers during their larval stage, while megalopodid and chrysomelid larvae feed on leaves or roots, either internally or externally, of both terrestrial and aquatic plants. The oldest known Chrysomeloidea fossil, attributed to the Cerambycidae, was found in the Lower Cretaceous Yixian Formation of China (Wang et al. 2014).

Chrysomeloidea contains diverse leaf-mining species across more than 40 genera (Jolivet and Hawkeswood 1995; Santiago-Blay 2004; Eiseman 2022; Frost 1924). Within Megalopodidae, at least a few *Zeugophora* species are leaf miners (Takemoto 2019). The Chrysomelidae family exhibits larval habits that vary from leaf mining and root boring to external leaf feeding. Among its ten subfamilies (Reid 1995), both Galerucinae and Cassidinae harbor leaf-mining species (Cai et al. 2022). Within Galerucinae in Japan, leaf-mining species have been identified in several genera, including *Phyllotreta* Chevrolat, 1837, *Mantura* Stephens, 1831, *Halticorcus* Lea, 1917 (= *Schenklingia*), *Argopistes* Motschulsky, 1860, *Argopus* Fischer von Waldheim, 1824, and *Sphaeroderma* Stephens, 1831 (Yano 1954, 1958, 1965; Kato 1991; Kimoto and Takizawa 1993). The Hispini tribe within Cassidinae span tropical and subtropical regions and exhibit several leaf-mining species (Chaboo 2007). Japanese Hispini leaf-mining species are found in the genera *Leptispa* Baly, 1858, *Asamangulia* Maulik, 1915, *Dactylispa* Weise, 1897, *Hispellinus* Weise, 1897, *Rhadiosa* Weise, 1905, *Platypria* Guérin-Méneville, 1840, and *Dicladispa* Gestro, 1897 (Kimoto and Takizawa 1993). Additionally, in the Notosacanthini within the subfamily Cassidinae, *Notosacantha* Chevrolat, 1837 also includes leaf-mining species (Rane et al. 2000; Monteith et al. 2021). Despite the abundance of taxonomic studies of chrysomelids in these genera (Kimoto and Takizawa 1993; Takizawa 2005, 2007, 2015, 2021), reports on their larval biology remain limited. Leaf mines of chrysomelids have been documented in just 15 species in Japan, as reported by Yano (1954, 1965) and Kato (1991). A more comprehensive understanding of the association between leaf-mining chrysomelids and their host plants could provide insights into the diversification processes within the Chrysomeloidea.

During the last 40 years, we have conducted extensive collections of Japanese leaf miners, reared them, and collected data on their diversity, host plants, and larval biology. In this article, we present a detailed account of this

leaf-mining beetle diversity, including the identification of two new chrysomelid species within the genera *Sphaeroderma* and *Dactylispa*. Additionally, we explore the host plants and host specificity of these leaf-mining species, with insights into leaf mines and their larval biology, and discuss the association between leaf-mining beetles and their host plants.

Our study reveals the presence of 64 leaf-mining species within Japanese Chrysomeloidea, each intricately associated with specific host plants. While most of these beetle species exhibit host specificity at the genus or species level, we have observed instances where certain species are associated with multiple genera belonging to phylogenetically distant plant families. By investigating whether these species demonstrate specialist or generalist tendencies, we have categorized the pattern of host selection as exhibiting extended host specificity.

Materials and methods

Since the 1980s, MK has conducted extensive sampling of chrysomelid leaf mines across the Japanese Archipelago and all specimens were collected by MK, with specific exceptions noted. To rear the leaf-mining chrysomelid larvae, mined leaves were placed in plastic cases with a layer of vermiculite at the bottom. This setup was kept moderately moist to create an optimal environment for the pupation and hibernation phases usually in incubators. Approximately 400 adult chrysomelid beetles were obtained by rearing the leaf-mining larvae. Leaves with leaf mines were dried as herbarium specimens and deposited in the Kyoto University Museum, Japan (**KUM**). Plant species were identified according to their scientific names, in line with Ohashi et al. (2015). The insect specimens were also deposited in the KUM, with the type specimens deposited in National Museum of Nature and Science, Tokyo (**NSMT**). All material with a registration number is mentioned in the listing of the designated material type.

For morphological examination, adult specimens were examined under a microscope (VHS-7000; Keyence, Osaka, Japan). This analysis was augmented by synthesizing virtual images from a series of depth-focused photographs to capture detailed images of the specimens. For identification we referred to Hayashi et al. (1984), Kimoto and Takizawa (1993, 1997). To observe male and female genitalia, the abdomens were macerated in in a 10% KOH solution for ~ 12 h at room temperature, rinsed in water, and dissected under a microscope.

Results

From the Japanese Archipelago, we confirmed 64 species of Chrysomeloidea as leaf miners, including two cerambycids, nine megalopodids, and 53 chrysomelids (Table 1). We provide a summary of host plants and leaf mines of these species and describe two new species belonging to *Sphaeroderma* and *Dactylispa*. The following list also includes ten beetle species that are unknown for their larval habits but are suspected to be leaf-miners in light of the habits of morphologically related species. In the following descriptions, families, subfamilies, tribes, and genera are arranged in a phylogenetic order suggested by Hayashi et al. (1984), and species in each genus are arranged in a taxonomic order of their host plants. In the genus *Dactylispa*, species are arranged by their species groups as suggested by Zhang et al. (2021).

Cerambycidae Latreille, 1802
Lamiinae Latreille, 1825
Mimectatina (Matsushita, 1933)

Mimectatina meridiana ohirai Breuning & Villiers, 1973
Fig. 1A–F

Host plant. Cycadaceae: *Cycas revoluta* Thunb. (Fig. 1B–F) (Kato 2001). The wood tissues of *Toddalia asiatica* (L.) and *Aucuba japonica* Thunb. are used as hosts (Coleopterological Society of Japan 1984).

Leaf mine. Linear or linear-blotch mines in the megasporophyll of female cycad plants (Fig. 1E). The larva sometimes penetrates the testa of the cycad seed. Pupation occurs within the mine on the leaf stalk of the megasporophyll (Fig. 1D, F). Frass is granular and deposited within the mine.

Material examined. • 25 adults, Hedo, Kunigami, Okinawa Is., Okinawa Pref., 1-II-1998 (collected as larva on *Cycas revoluta*), emerged on 3-III–20-VI-1998; • 7 adults, Hedo, Kunigami, Okinawa Is., Okinawa Pref., 10-III-1997 (as larva on *C. revoluta*), emerged on 25-IV–20-VI-1997; 2 adults, Hedo, Kunigami, Okinawa Is., Okinawa Pref., 19-IV-2000 (as larva on *C. revoluta*), emerged on ?-V-2000; • 8 adults, Angyaba, Kakeroma Is., Setouchi, Kagoshima Pref., 10-V-2001 (as larva on *C. revoluta*), emerged on 12–28-VI-2001.

Sybra Pascoe, 1865

Sybra ordinata Bates, 1873
Fig. 1G–I

Host plant. Cycadaceae: *Cycas revoluta* (Fig. 1H, I) (Kato 2001). Wood of *Ficus superba* (Miq.), *Ficus erecta* Thunb., *Pittosporum tobira* (Thunb.), and *Boehmeria biloba* Wedd. are also used as larval hosts (Coleopterological Society of Japan 1984).

Leaf mines. Linear mine in a leaf stalk. The adult female bites the lower surface of the leaf stalk and inserts eggs into the scar (Fig. 1H). The larva mines the woody leaf stalk linearly, but does not enter leaflets. The fully grown larva pupates in the mine (Fig. 1I).

Material examined. • 5 adults, Haneji, Nago, Okinawa Is., Okinawa Pref., 1-II-1998 (as larva on *Cycas revoluta*), emerged on ?-V-1998; 2 adults, Hedo, Kunigami, Okinawa Is., Okinawa Pref., 1-II-1998 (as larva on *Cycas revoluta*), emerged on 20-III-1998.

Megalopodidae Latreille, 1802
Zeugophorinae Böving & Craighead, 1931
Zeugophora Kunze, 1818

Zeugophora annulata (Baly, 1873)
Fig. 2N–Q

Host plant. Celastraceae: *Celastrus orbiculatus* Thunb., *Euonymus alatus* (Thunb.), *E. fortunei* (Turcz.), *E. japonicus* Thunb., *E. macropterus* Rupr.,

E. melananthus (Thunb.), *E. oxyphyllus* Miq., *E. tricarpus* Koidz., *E. sieboldianus* Blume. *Tripterygium regelii* is also recorded as a host by Takemoto (2019).

Leaf mine. Full-depth linear-blotch mine on newly-opened leaf (Fig. 2O–Q). The mine often covers the whole area of the leaf causing deformation of the leaf, and the larva moves to another unmined leaf. Frass is thread-like and meandering, deposited along the center of the mine. The fully grown larva exits the mined leaf, falls to the ground, and pupates underground.

Material examined. • 4 adults, Iyari, Ômachi, Nagano Pref., 5-V-2016 (as larva on *Euonymus alatus*), emerged on 27-V-2016 (Fig. 2N, O); 5 adults, Saroma Lake, Yûbetsu, Hokkaidô, 5-VI-2016 (as larva on *E. sieboldianus*), emerged on 29–30-VI-2016; 3 adults, Mt. Tara, Isahaya, Nagasaki Pref., 19-IX-2017 (as larva on *E. melananthus*), emerged on 23-V-2017 (Fig. 2P); • 2 adults, Mt. Myôjô, Niigata Pref., Aoi-ku, Shizuoka Pref., 9-V-2018 (as larva on *E. fortunei*), emerged on 10-VI-2018 (Fig. 2Q); • 1 adult, Mt. Teine, Sapporo, Hokkaido, 6-VI-2016 (as larva on *E. tricarpus*), emerged on 25-VI-2016; • 2 adults, Ashiu, Nantan, Kyoto Pref., 5-V-1992 (as larva on *E. oxyphyllus*), emerged on ?-V-1992; • 1 adult, Hidakatsu, Tsushima Is., Nagasaki Pref., 19-IV-2009 (as larva on *E. japonicus*), emerged on 18-V-2009; • 1 adult and many leaf mines, Mt. Byôbu, Kizukuri, Aomori Pref., 14-V-1993 on *E. macropterus*; • 3 adults, Misakubo Dam, Hamamatsu, Shizuoka Pref., 10-V-2000 (as larva on *Celastrus orbiculatus* collected by T. Kato), emerged on 7-VI-2000.

Zeugophora chujoi Ohno, 1961
Fig. 2F–I

Host plant. Celastraceae: *Euonymus fortunei* (Turcz.).

Leaf mine. Full-depth linear-blotch mine on the leaf blade and the midrib of a newly-opened leaf (Fig. 2G–I). The egg is laid in the midrib and the hatched larva enters the midrib and bores into the petiole, leading to leaf abscission from the shoot at the petiole base. Following the leaf fall, the mine diverges from the midrib and expands in the leaf blade, forming a blotch mine. Frass is granular and scattered throughout the mine. The fully grown larva exits the mined leaf, falls to the ground, and pupates underground.

Material examined. • 4 adults, Nagao-tôge, Gotenba, Shizuoka Pref., 15-V-2018 (as larva on *Euonymus fortunei*), emerged on 18-VI-2018 (Fig. 2F–I).

Zeugophora flavonotata (Chûjô, 1935)
Fig. 2J–M

Host plant. Celastraceae: *Euonymus carnosus* Maxim., *E. japonicus* Thunb.

Leaf mine. Full-depth linear mine on the newly-opened leaf (Fig. 2K–M). The egg is laid near the leaf margin and the hatched larva mines along the leaf margin, slowly expanding the mine. Frass is thread-like, deposited somewhat to one side of the center. The fully grown larva exits the mined leaf, falls to the ground, and pupates underground.

Material examined. • 2 adults, Yutsun, Iriomote Is., Yaeyama, Okinawa Pref., 24-III-2022 (as larva on *Euonymus carnosus*), emerged on 16–18-IV-2022 (Fig. 2J–L); 3 adults, Todomari, Iriomote Is., Yaeyama, Okinawa Pref.,

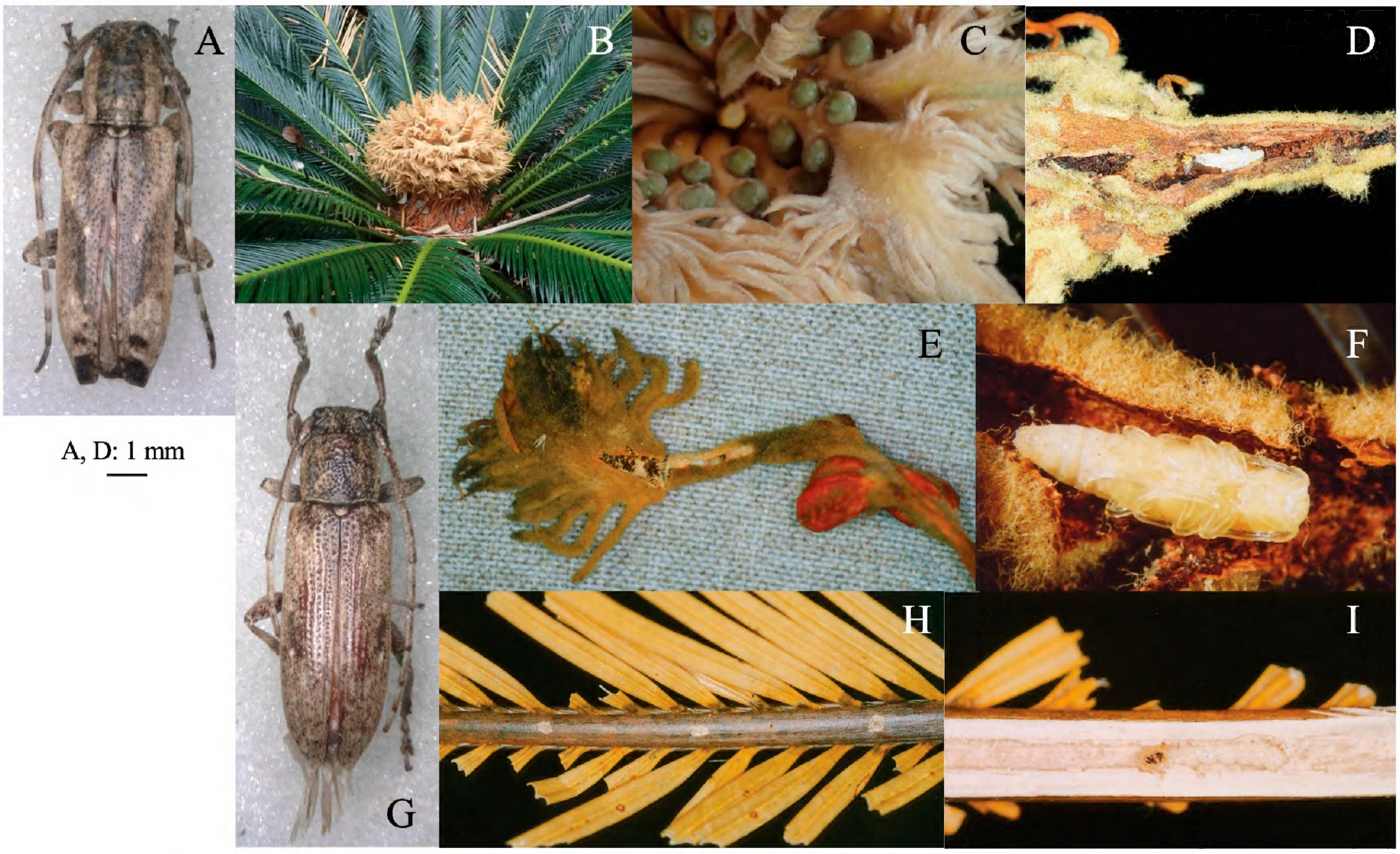

Figure 1. Two cerambycid species associated with *Cycas revouta: Mimectatina meridiana ohirai* (**A–F**) and *Sybra flavostriata flavostriata* (**G–I**). **A, G** adult habitus **B** flowering cycad **C** flowering megasporophyll **D** cross section of mined megasporophyll **E** mine of megasporophyll **F** pupa in the mine **H** oviposition scars on leaf stalk **I** larva mining the leaf stalk.

27-III-2018 (as larva on *E. carnosus*), emerged on 16–18-IV-2018; 14 adults, Hoshidate, Iriomote Is., Yaeyama, Okinawa Pref., 6-III-2019 (as larva on *E. japonicus*), emerged on 3–6-IV-2019 (Fig. 2M).

Zeugophora nigricolis **(Jacoby, 1885)**

Fig. 2C–E

Host plant. Celastraceae: *Euonymus sieboldianus* Blume.

Leaf mine. Upper-layer ophiogenous blotch mine on the mature leaf (Fig. 2D, E). Within the blotch, the larval trajectory itself is linear and meandering compactly. The egg is laid along the basal margin of the leaf and the hatched larva mines along the leaf margin, abruptly expanding the mine. Within the blotch, the larval trajectory itself is linear and meandering compactly. Frass is granular and deposited along the meandering trajectory. The fully grown larva exits the mined leaf, falls to the ground, and pupates underground.

Material examined. • 2 adults, Sugadaira, Ueda, Nagano Pref., 18-VI-2017 (as larva on *Euonymus sieboldianus*), emerged on 20–28-VII-2017 (Fig. 2C–E).

Zeugophora unifasciata **(Jacoby, 1885)**

Fig. 2A, B

Host plant. Celastraceae: *Euonymus sieboldianus*.

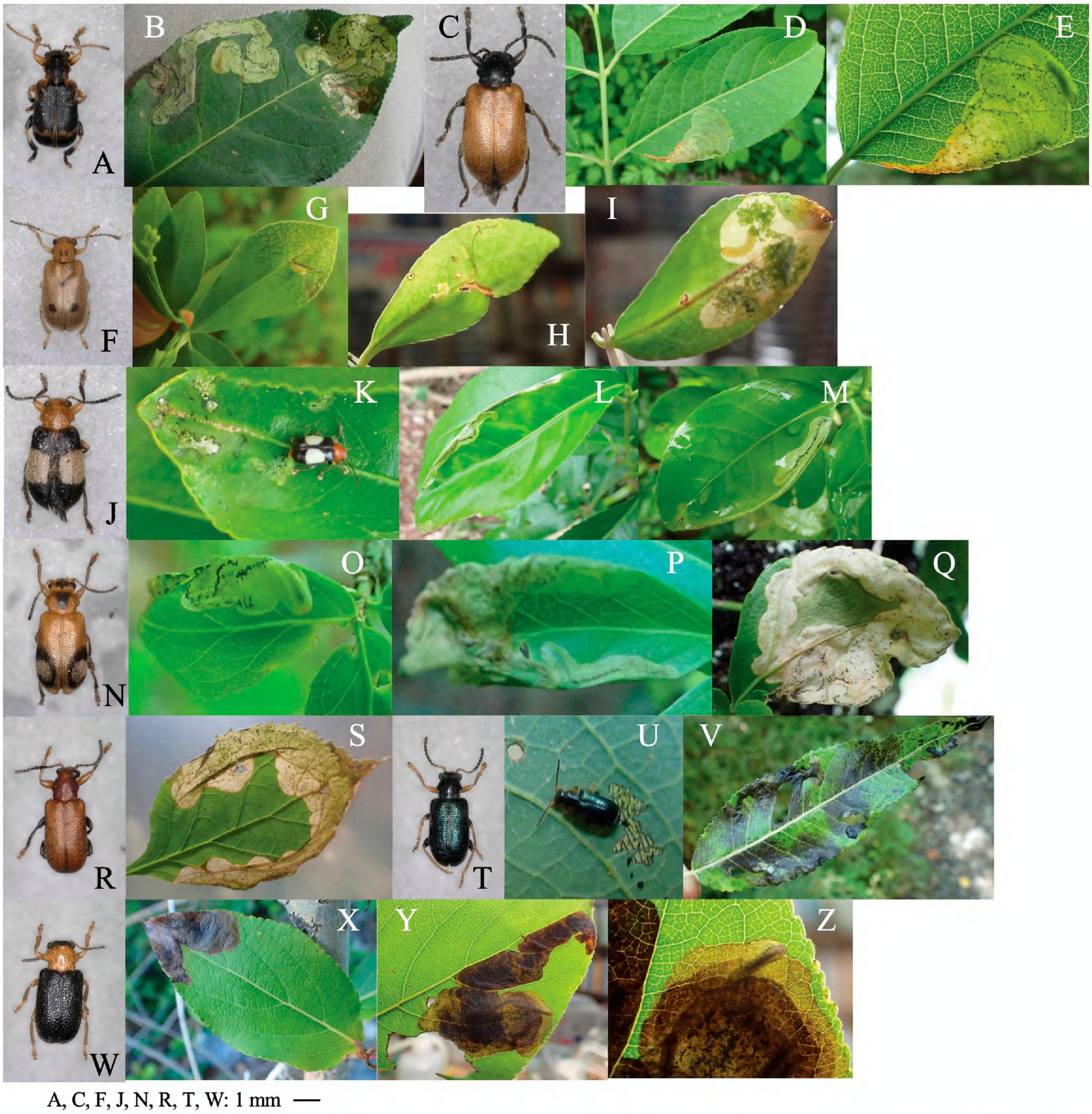

Figure 2. Habitus and feeding scars of adult beetles and leaf mines of eight *Zeugophora* species **A, B** *Z. nigricolis* **C–E** *Z. unifasciata* **F–I** *Z. chujoi* **J–M** *Z. flavonotata* **N–Q** *Z. annulata* **R, S** *Z. varipes* **T–V** *Z. hozumii* **W–Z** *Z. japonica*. Host plants **A, B** *Euonymus sieboldianus* at Hirayu, Gifu Pref. **C–E** *E. sieboldianus* at Sugadaira, Nagano Pref. **F–I** *E. fortunei* at Nagao-toge, Shizuoka Pref. **J–L** *E. tanakae* at Yutsun, Iriomote Is., Okinawa Pref. **M** *E. japonicus* at Hoshidate, Iriomote Is., Okinawa Pref. **N, O** *E. alatus* at Kiyosato, Yamanashi Pref. **P** *E. melananthus* at Mt. Tara, Nagasaki Pref. **Q** *E. fortunei* at Mt. Myôjô, Niigata Pref. **R, S** *Symplocos sawafutagi* at Iyari, Nagano Pref. **T–V** *Salix cardiophylla* var. *urbaniana* at Kitazawa-toge, Nagano Pref. **W–Z** *Populus suaveolens* at Sôunkyô, Hokkaido.

Leaf mine. Upper-layer linear mine on mature leaf (Fig. 2B). The egg is laid in the leaf blade and the hatched larva construct slightly meandering mine. Width of the mine is slightly wider than the width of the larva. Frass is thread-like, deposited along the meandering trajectory. The fully grown larva exits the mined leaf, falls to the ground, and pupates underground.

Material examined. • 5 adults, Hirayu-tôge, Takayama, Gifu Pref., 6-IX-2019 (as larva on *Euonymus sieboldianus*), emerged on 6–7-X-2019 (Fig. 2A, B); • 1 adult, Toyohara, Nasu, Tochigi Pref., 2-VII-2022 (as larva on *E. sieboldianus*), emerged on 3-VIII-2022.

Zeugophora varipes (Jacoby, 1885)

Fig. 2R, S

Host plant. Symplocaceae: *Symplocos coreana* (H. Lev.), *S. sawafutagi* Nagam.

Leaf mine. Full-depth linear-blotch mine on young leaf (Fig. 2S). The egg is laid in the leaf blade, and the hatched larva constructs linear mine along the leaf margin, then gradually expands the mine. The mine is wider than the width of the larva. Frass is granular, scattered throughout the mine. The fully grown larva exits the mined leaf, falls to the ground, and pupates underground.

Material examined. • 1 adult and 5 leaf mines, Iyari, Ômachi, Nagano Pref., 5-V-2016 on *Symplocos sawafutagi* (Fig. 2R, S); 6 adults, Omotsubo, Okayama Pref., 27-V-1993 (as larva on *Symplocos coreana*), emerged on 20–24-VI-1993.

Zeugophora hozumii Chûjô, 1953

Fig. 2T–V

Host plant. Salicaceae: *Salix cardiophylla* Trautv. et C. A. Mey. Although Takemoto (2019) lists *Salix caprea* L. as a host plant, this record is not confirmed.

Leaf mine. Black upper-layer linear-blotch mine on mature leaf (Fig. 2V). The egg is laid in the leaf blade, and the hatched larva constructs a linear-blotch mine, the upper surface of which turns black. Frass is granular, scattered throughout the mine. The fully grown larva exits the mined leaf, falls to the ground, pupates underground, and hibernates as a pupa.

Material examined. • 8 adults and many leaf mines, Kitazawa Tôge, Ina, Nagano Pref., 30-VII-2016, feeding lower surface of leaf of *Salix cardiophylla* (Fig. 2T–V); • 1 adult, Azusa-gawa, Matsumoto, Nagano Pref., 24-X-2020 (as larva on *Salix cardiophylla*), emerged on 22-III-2021.

Zeugophora japonica Chûjô, 1951

Fig. 2W–Z

Host plant. Salicaceae: *Populus suaveolens* Fisch.

Leaf mine. Black upper-layer blotch mine on mature leaf, sometimes gregarious (Fig. 2X–Z). The egg is laid along the leaf margin, and the hatched larva constructs a blotch mine, the upper surface of which turns black. Frass is granular, scattered throughout the mine. The fully grown larva exits the mined leaf, falls to the ground, pupates underground.

Material examined. • 1 adult, Rekifune Nakanokawa, Taiki, Tokachi, Hokkaidô, 23-VI-2017 (as larva on *Populus suaveolens*), emerged on 21-VIII-2017 (Fig. 2W–Z); • 2 adults, Rubeshibe, Kitami, Hokkaidô, 25-VI-2017 (as larva on *P. suaveolens*), emerged on 21-VIII-2017.

***Zeugophora cupka* Takemoto, 2019**

Host plant. Salicaceae: *Populus suaveolens* (Takemoto 2019). Leaf mine has not yet been reported.

***Zeugophora gracilis* Chûjô, 1958**

Note. There is no recent collection of this species, and its host plant and mine are not known (Takemoto 2019).

Chrysomelidae Latreille, 1802
Galerucinae Latreille, 1802
Alticini Newman, 1834
***Phyllotreta* Chevrolat, 1836**

***Phyllotreta ezoensis* Kimoto, 1993**
Fig. 3A–I

Host plant. Brassicaceae: *Draba nemorosa* L. The host plant grows on levee of traditional rice fields and upland fields in Central Honshu (Fig. 3C).

Leaf mine. Full-depth linear mine of leaf blade, midrib, petiole, and shoot (Fig. 3D–I). The egg is laid on the leaf, and the hatched larva mines toward the midrib, and reenters midrib/leaf blade. Larvae repeats mining leaf and mining midrib, petiole, and/or shoot, often by exiting its mine and establishing

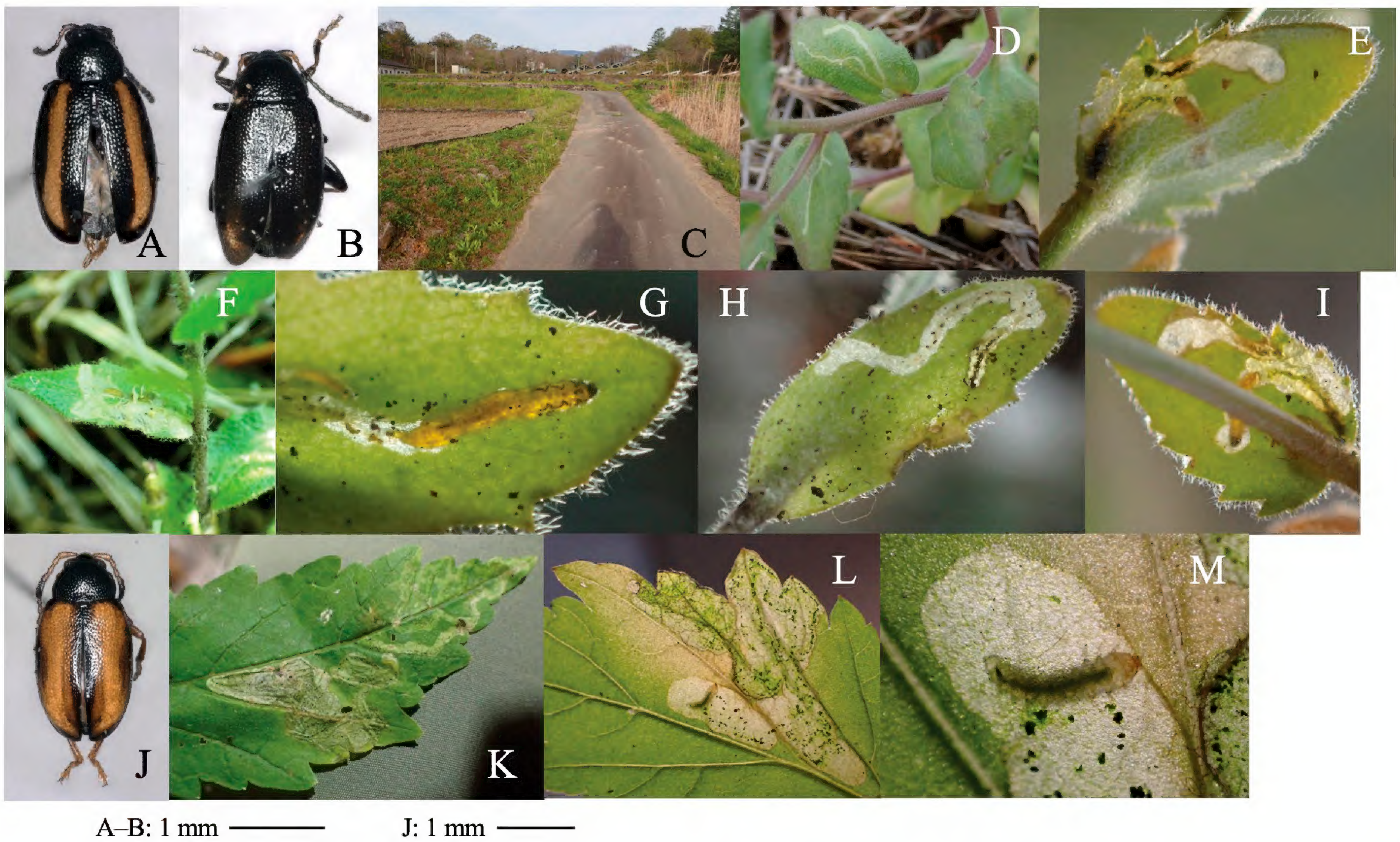

Figure 3. Habitus of adults and leaf mines of two *Phyllotreta* species **A–I** *P. ezoensis* **J–M** *P. shirahatai*. Host plants **A–I** *Draba nemorosa* at Kiyosato, Yamanashi Pref. **J–M** *Cardamine appendiculata* at Eniwa (**J, K**) and Tobai (**L, M**), Hokkaido.

a new mine. Frass is granular, deposited linearly along midline of the mine. The fully grown larva exits the mined leaf, falls to the ground, and pupates underground. The adult emerges ~ 2 weeks after pupation, and varies in elytral pattern (Fig. 3A, B).

Material examined. • 6 adults, Matsubara-Lake, Koumi, Nagano Pref. 21-V-2021 (as larva on *Draba nemorosa*), emerged on 4-VI-2021 (Fig. 3A–E); • 15 adults, Kiyosato, Hokuto, Yamanashi Pref., 4-V-2022 (as larva on *D. nemorosa*), emerged on 17–20-V-2022 (Fig. 3F–I).

Phyllotreta shirahatai **Madar, 1959**
Fig. 3J–M

Host plant. Brassicaceae: *Cardamine leucantha* (Tausch.).

Leaf mine. Full-depth linear-blotch mine on mature leaf (Fig. 3K–M). Frass is granular, scattered throughout the mine. The fully grown larva exits the mined leaf, falls to the ground, and pupates underground.

Material examined. • 1 adult and several leaf mines on *Cardamine leucantha*, Eniwa Park, Eniwa, Hokkaidô, 21-VII-2020 (Fig. 3J, K); several leaf mines, Tôbai, Nemuro, Hokkaidô, 2-VIII-2023 on *C. leucantha* (Fig. 3L, M).

Longitarsus **Latreille, 1829**

Longitarsus **aff.** ***holsaticus*** **(Linnaeus, 1758)**
Fig. 4A–G

Note. Whereas six collected specimens were tentatively identified as this species, more specimens and further taxonomic studies are necessary.

Host plant. Plantaginaceae: *Pennellianthus frutescens* (Lamb.). Host plants of *Longitarsus holsaticus* are reported to be *Veronica* spp. by Kimoto and Takizawa (1993).

Leaf mine. Full-depth linear or radiate mine in young leaf (Fig. 4F–G). Frass is deposited compactly in a few parts of the mine, and sometimes discharged from the mine through holes perforated along the mine edge. The fully grown larva exits the mined leaf, falls to the ground, and pupates underground.

Material examined. • 6 adults, Mt. Tarumai, Chitose, Hokkaidô, 4-VII-2010 (as larva on *Pennellianthus frutescens*), emerged on 17-VIII-2010 (Fig. 4A–G).

Dibolia **Latreille, 1829**

Dibolia japonica **S.-H. Chen, 1933**
Fig. 4H–L

Host plant. Lamiaceae: *Stachys aspera* Michx.

Leaf mine. Full-depth linear-blotch mine on mature leaf (Fig. 4J–L). Frass is thread-like, deposited along trajectory in the mine. The fully grown larva exits the mined leaf, falls to the ground, pupates underground.

Material examined. • 1 adult, Shôji-ko Lake, Fuji-kawaguchiko, Yamanashi Pref., 4-VII-2010 (as larva on *Stachys aspera*), emerged on 3-VIII-2010 (Fig. 4H–L).

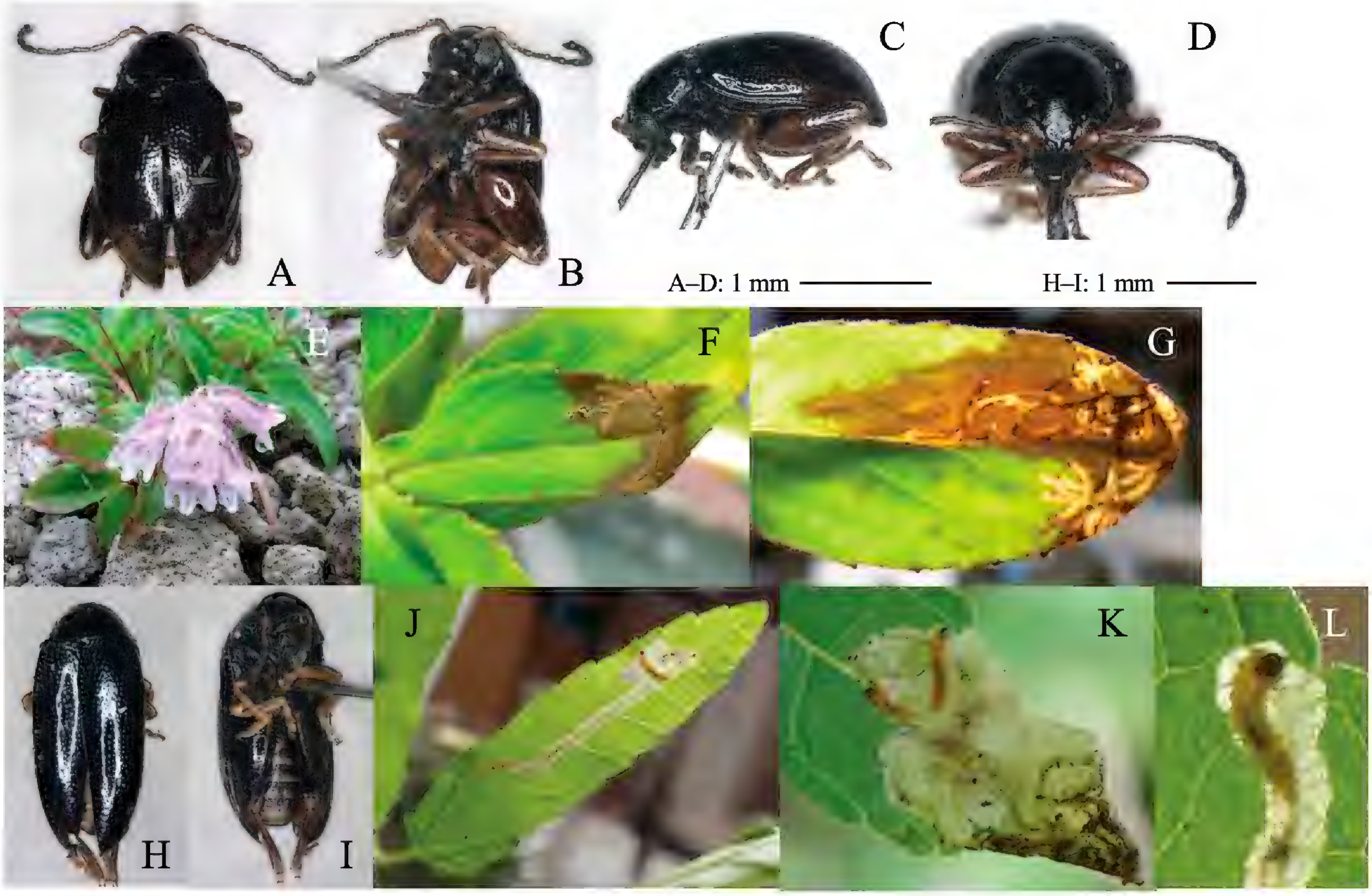

Figure 4. Habitus of adults and leaf mines of two species belonging to two Alticini genera, *Longitausus and Dibolia* **A–G** *Longitarsus holsaticus* **H–L** *Dibolia japonica*. Host plants **A–G** *Pennellianthus frutescens* at Mt. Tarumae, Hokkaido **H–L** *Stachys aspera* var. *hispidula* at Lake Shoji-ko, Yamanashi Pref.

***Mantura* Stephens, 1831**

***Mantura clavareaui* Heikertinger, 1912**
Fig. 5A–I

Host plant. Polygonaceae: *Rumex japonicus* Houtt., *Polygonum aviculare* L. *Rumex acetosa* L. is also recorded as a host plant (Kimoto and Takizawa 1993).

Leaf mine. Full-depth linear mine occurs on mature leaf (Fig. 5D–F, I). The larva alternates mining the leaf blade and mining the midrib, the petiole, and the shoot, and often relocates its mine. Frass is granular, deposited linearly along middle line of the mine. The fully grown larva exits the mined leaf, falls to the ground, and pupates underground.

Material examined. • 3 adults, Kôda, Notojima Is., Nanao, Ishikawa Pref. 2-V-2023 (as larva on *Rumex japonicus*), emerged on 22-V-2023 (Fig. 5A–F); • 21 adults, Kamematsu, Shivani, Kumamoto Pref., 28-IV-2017 (as larva on *R. japonicus*), emerged on 13–14-V-2017; • 14 adults, Mihonoseki, Matsue, Shimane Pref., 15-V-2006 (as larva on *Polygonum aviculare*), emerged on 31-V–3-VI-2006 (Fig. 5G–I).

***Mantura fulvipes* Jacoby, 1885**
Fig. 5J–L

Host plant. Oxalidaceae: *Oxalis corniculata* L.

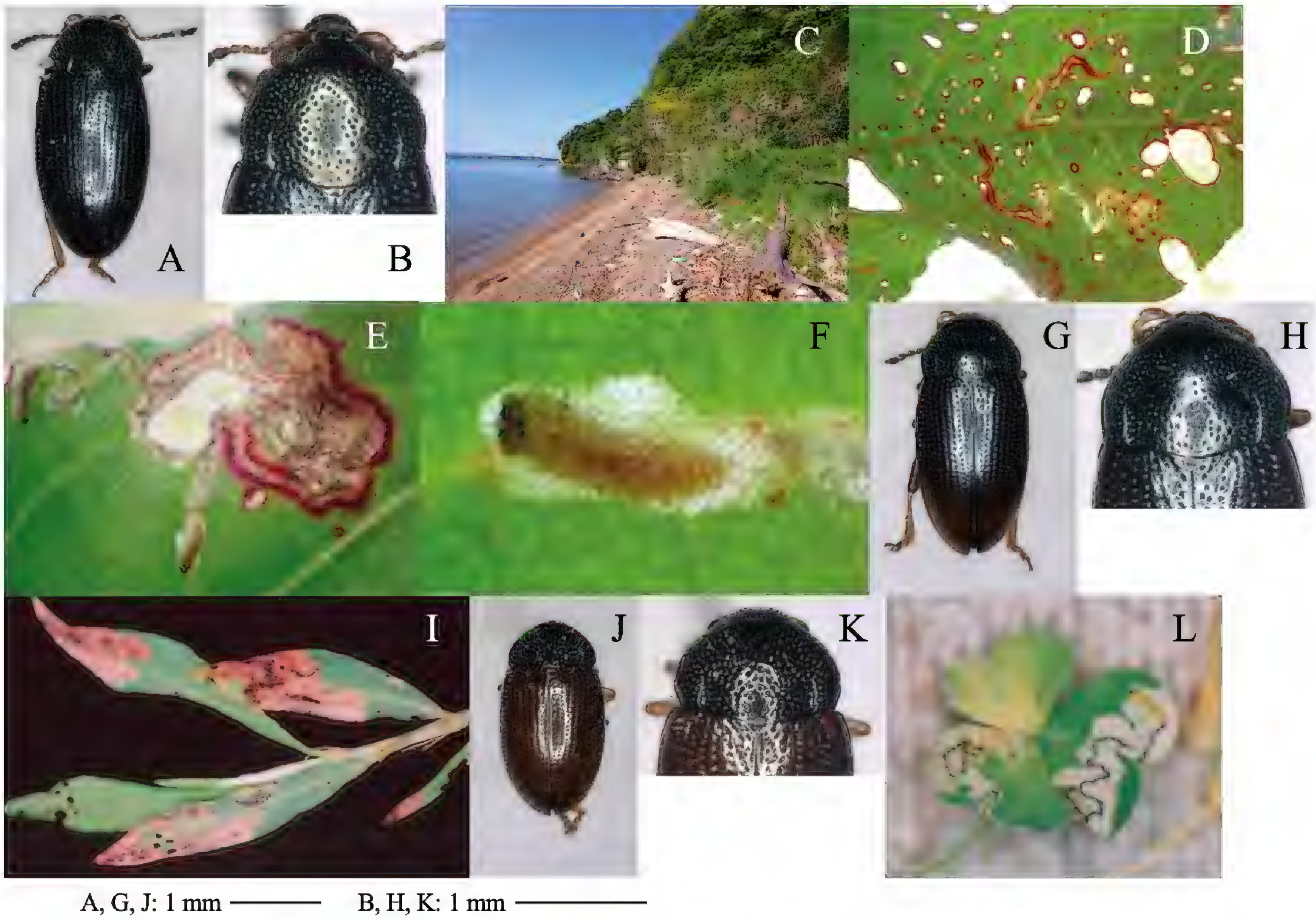

Figure 5. Habitus of adults, habitat, and leaf mines of two *Mantura* species **A–I** *M. clavareaui* **J–L** *M. fulvipes*. Host plants **A–F** *Rumex japonicus* at Notojima Island, Ishikawa Pref. **G–I** *Polygonum aviculare* at Mihogaseki, Shimane Pref. **J–L** *Oxalis corniculata* at Tamanoura, Fukue Is., Nagasaki Pref.

Leaf mine. Full-depth linear mine on mature leaf (Fig. 5L). The egg is laid along the leaf margin, and hatched larva mines along the leaf margin, gradually expanding the mine. Width of the mine is wider than that of larva. Frass is thread-like, deposited along middle line of the mine. The fully grown larva exits the mined leaf, falls to the ground, pupates underground.

Material examined. • 19 adults, Tamanoura, Fukue Is. Goto, Nagasaki Pref. 9-X-1998 (as larva on *Oxalis corniculata*), emerged on 22–26-X-1998 (Fig. 5J–L).

Mantura japonica Jacoby, 1885

Note. Host plant has not been reported (Hayashi et al. 1984; Kimoto and Takizawa 1993).

Hippuriphila Foudras, 1859

Hippuriphila babai (Chûjô, 1959)

Fig. 6A–F

Host plant. Equisetaceae: *Equisetum arvense* L., *E. fluviatile* L.

Leaf mine. Full-depth or internal linear mine on leaf-like branch and the green stem (Fig. 6B–E). The larva is cylindrical (Fig. 6F) and sometimes exits its mine and moves to the other shoot. Frass is thread-like, deposited in the mine.

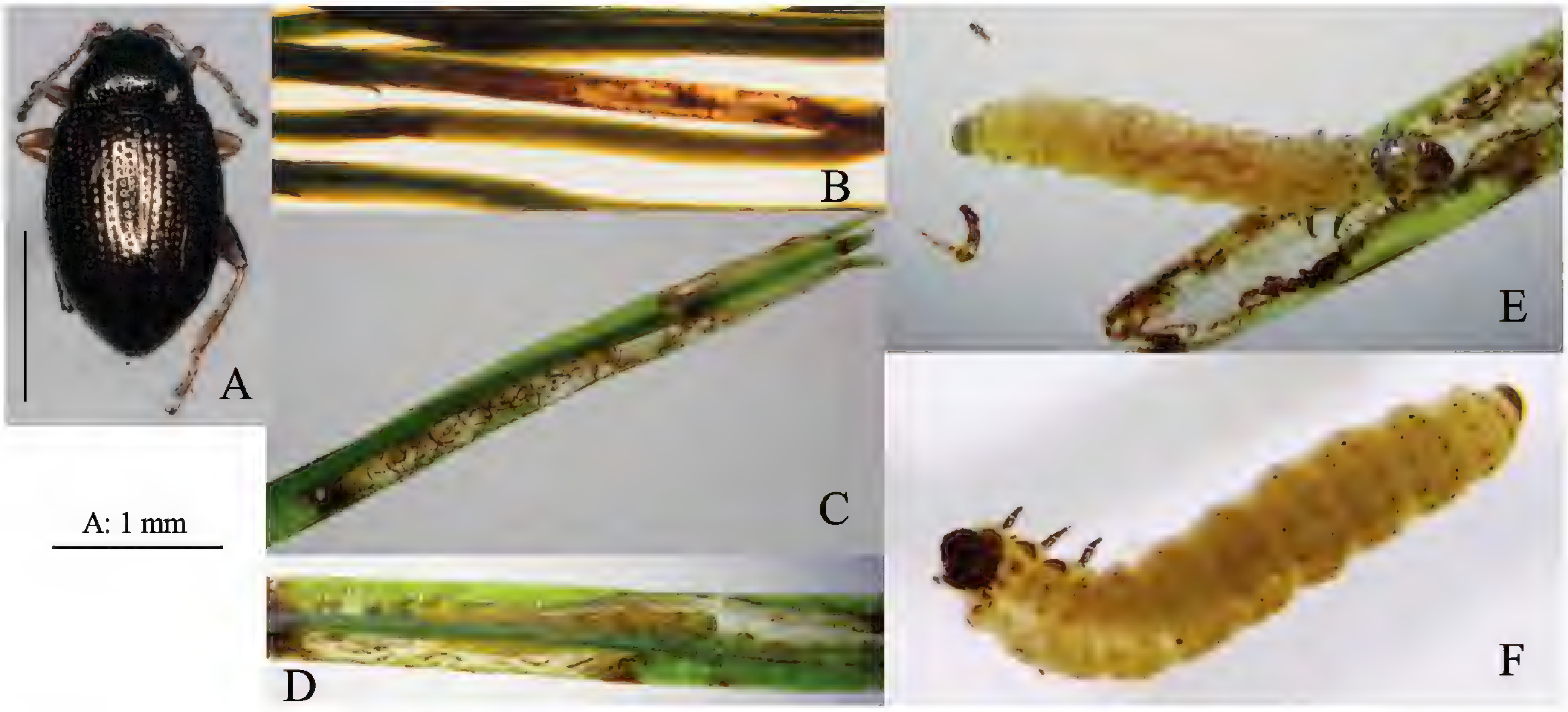

Figure 6. Habitus of adults, leaf mine, and larva of *Hippuriphila babai* on *Equisetum arvense* **A** habitus of adults **B, C** leaf-mine at Mt. Teine **D–F** larva at Yubari, Hokkaido.

Material examined. • 2 adults, Mt. Teine, Sapporo, Hokkaidô, 9-X-1998 (as larva on *Equisetum arvense*), emerged on 25-VII–3-VIII-1998 (Fig. 6A–C); • 2 adults, Rebun Is., Hokkaidô, 9-VII-1995 (as larva on *E. arvense*), emerged on 25–27-VII-1995; • 5 adults, Bibi, Chitose, Hokkaidô, 30-VI-2023 (as larva on *E. fluviatile*), emerged on 17–20-VII-2023.

Psylliodes Latreille, 1829

Psylliodes punctifrons Baly, 1874

Fig. 7A–P

Host plant. Brassicaceae: *Brassica juncea* (L.), *Raphanus sativus* L. var. *raphanistroides* (Makino), *Rorippa palustris* (L.), *Eutrema japonicum* (Miq.). *Cardamine anemonoides*, *Brassica chinensis* and *B. napus* are also recorded as host plants (Takizawa 2005).

Leaf mine. Full-depth linear mine occurs on leaf blade, midrib, petiole, and shoot (Fig. 7C–E, H, I, L–P). The egg is laid on the leaf, and the hatched larva mines toward midrib, and reenters leaf blade. Larvae alternates mining the leaf and mining the midrib/petiole/shoot, and often relocates its mine. Frass is deposited compactly in a few parts of the mine, and sometimes discharged from the mine through the perforated holes. The fully grown larva exits the mined leaf, falls to the ground, pupates underground. Adult emerges ~ 1 month after pupation. On *Eutrema japonicum* with long petiole, linear mine of petiole and midrib of mature leaf (Fig. 7L–P). The mined petiole turns blackish. Frass is deposited compactly in a few parts of the mine, and sometimes discharged from the mine through perforated holes.

Material examined. • 23 adults, Kusauchi, Kizu-gawa, Kyôtanabe, Kyoto Pref. 11-III-2020 (as larva on *Brassica juncea*), emerged on 1–15-V-2020 (Fig. 7A–E); • 1 adult, Kôda, Notojima Is., Nanao, Ishikawa Pref., 2-V-2023 (as larva on *Raphanus sativus* var. *raphanistroides*), emerged on 4-VI-2023 (Fig. 7G–J); • 2 adults, Watarase, Fujioka, Tochigi Pref., 25-V-2020 (as larva on *Rorippa palustris*),

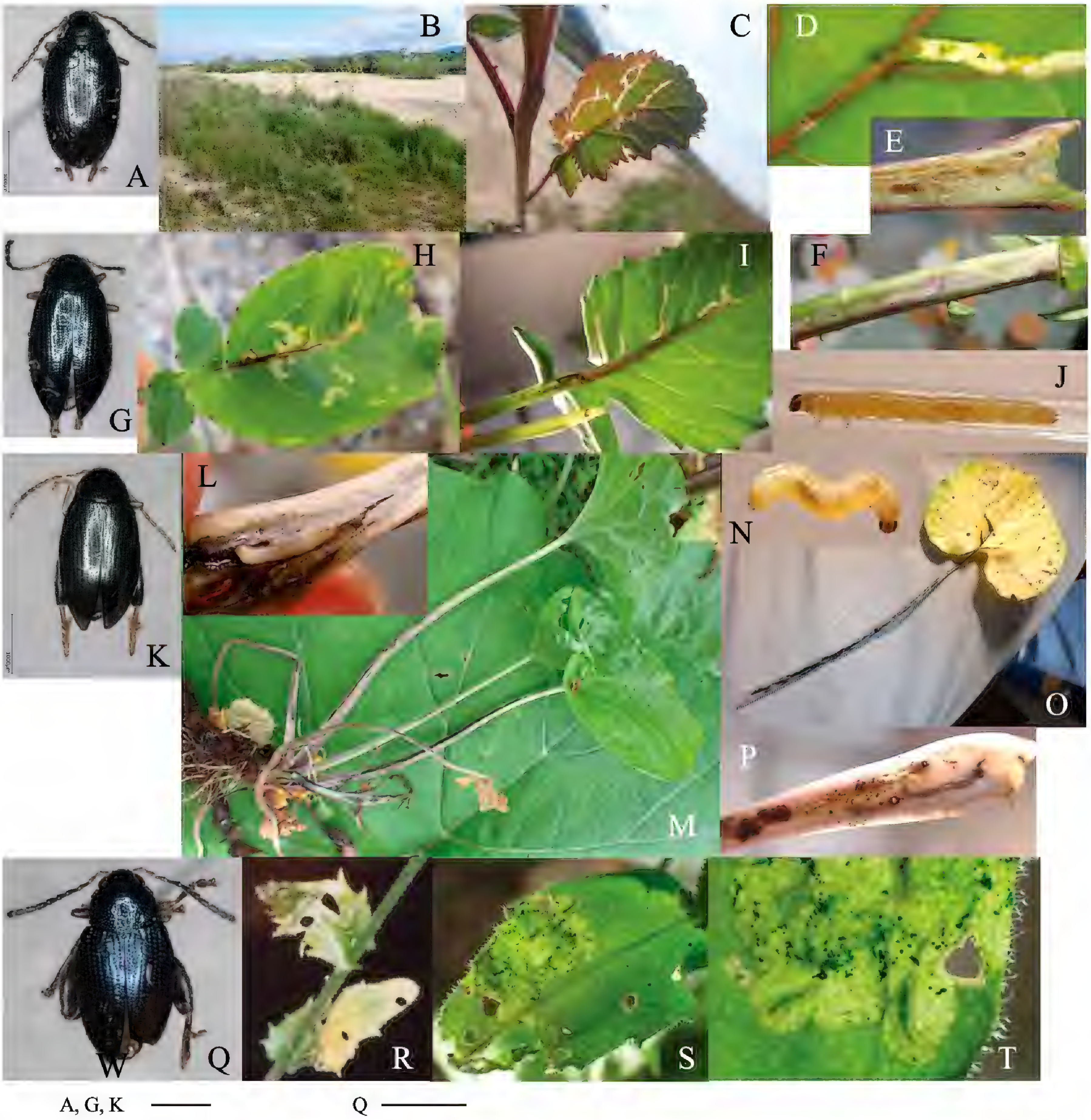

Figure 7. Habitus of adults and larvae, habitat, and leaf mines of three *Psylliodes* species **A–J** *P. punctifrons* **K–P** *P. sasakii* **Q–T** *P. subrugosa*. Host plants **A–F** *Brassica juncea* at Kizu-gawa, Kyôto **G–I** *Raphanus sativus* var. *hortensis* at Notojima Is., Ishikawa Pref. **K–M** *Eutrema japonicum* at Futamata, Oshamanbe, Hokkaido **N–P** *Eutrema japonicum* at Nyûkawa, Takayama, Gifu Pref. **Q–T** *Arabis hirsuta* at Shimo-suwa, Nagano Pref.

emerged on 8–14-VI-2020; • 19 adults, Futamata, Oshamanbe, Hokkaidô, 20-V-2023 (as larva on *Eutrema japonicum*), emerged on 14–25-VI-2023 (Fig. 7K–M); • 2 adults, Nyû-kawa, Takayama, Gifu Pref., 1-V-2023 (as larva on *Eutrema japonicum*), emerged on 29-V–5-VI-2023 (Fig. 7N–P).

***Psylliodes* aff. *subrugosa* Jacoby, 1885**
Fig. 7Q–T

Note. Two female specimens were reared and tentatively identified as related to this species, but there is a possibility that this is an undescribed species.

Host plant. Brassicaceae: *Arabis hirsuta* (L.). Crucifers are known as host plants (Kimoto and Takizawa 1993), while its biology has not been reported.

Leaf mine. Linear mine in the midrib and the petiole of mature leaf (Fig. 7R–T). The egg is laid on the petiole, and the hatched larva mines the petiole, and sometimes enter the midrib. The mined petiole becomes blackish. Frass is deposited compactly in a few parts of the mine, and sometimes discharged from the mine through perforated holes. The fully grown larva (Fig. 7N) exits the mined leaf, falls to the ground, and pupates underground. The adult emerges ~ 1 month after pupation.

Material examined. • 2 adults, Higashimata, Shimosuwa, Suwa-gun, Nagano Pref., 28-VI-2020 (as larva on *Arabis hirsuta*), emerged on 9-VIII-2020 (Fig. 7Q, S, T): several leaf mines on *Arabis hirsuta*, Sanjiro, Matsumoto, Nagano Pref., 28-VII-1995 (Fig. 7R).

Halticorcus Lea, 1917

Halticorcus kasuga (Nakane, 1963)

Fig. 8A–H

Host plant. Polypodiaceae: *Lepisorus miyoshianus* (Makino)., *L. onoei* (Franch. et Sav.), *L. thunbergianus* (Kaulf.), *Pyrrosia linearifotia* (Hook.) and *Lemmaphyllum microphyllum* C. Presl. are reported as adult's host plants by Suzuki et al. (2008).

Leaf mine. Upper-layer linear-blotch mine on mature leaf (Fig. 8B, F, G). The fully grown larva (Fig. 8H) exits the mined leaf, falls to the ground, and pupates underground.

Material examined. • 3 adults, Mt. Shizuhata, Aoi-ku, Shizuoka Pref., 27-VII-2017 (as larva on *Lepisorus thunbergianus*), emerged on 12–18-IX-2017 (Fig. 8A, B); • 1 adult on *L. onoei*, Shôji-ko Lake, Fuji-kawaguchi-ko, Yamanashi Pref., 8-IX-2019 (Fig. 7C); • 2 adults, Shimo-shimizu, Kiso-fukushima, Nagano Pref., 7-VIII-2011 (as larva on *L. miyoshianus*), emerged on 4-IX-2011 (Fig. 7D–H).

Halticorcus sauteri (S.-H. Chen, 1934)

Fig. 8I–O

Host plant. Dryopteridaceae: *Cyrtomium falcatum* (L. f.); Oleandraceae: *Nephrolepis cordifolia* (L.); Polypodiaceae: *Colysis elliptica* (Thunb.), *Loxogramme salicifolia* (Makino), *Leptochilus neopothifolius* Nakaike, *Lemmaphyllum microphyllum* Presl., *Microsorum buergerianum* (Miq.), *Phymatosorus scolopendria* (Burm. f.). *Thelypteris acuminata* (Houtt.) is also reported as adult's host plants by Suzuki et al. (2008).

Leaf mine. Upper-layer linear-blotch mine on mature leaf (Fig. 8J–L, N, O). Frass is thread-like, thin, and often intermittent, and deposited along the meandering larval trajectory. The fully grown larva exits the mined leaf, falls to the ground, and pupates underground.

Material examined. • 1 adult and several leaf mines, Imasato, Uken, Amami-ôshima Is. Kagoshima Pref., 4-IX-2011 on *Cyrtomium falcatum* (Fig. 8K, L); • 2 adults, Angyaba, Tatsugô, Amami-ôshima Is. Kagoshima Pref., 8-V-1997 (as larva on *Cyrtomium falcatum*), emerged on 22-VI-1997; • 22 adults, Kinsakubaru, Naze, Amami-ôshima Is. Kagoshima Pref., 3-VI-1996 (as larva on

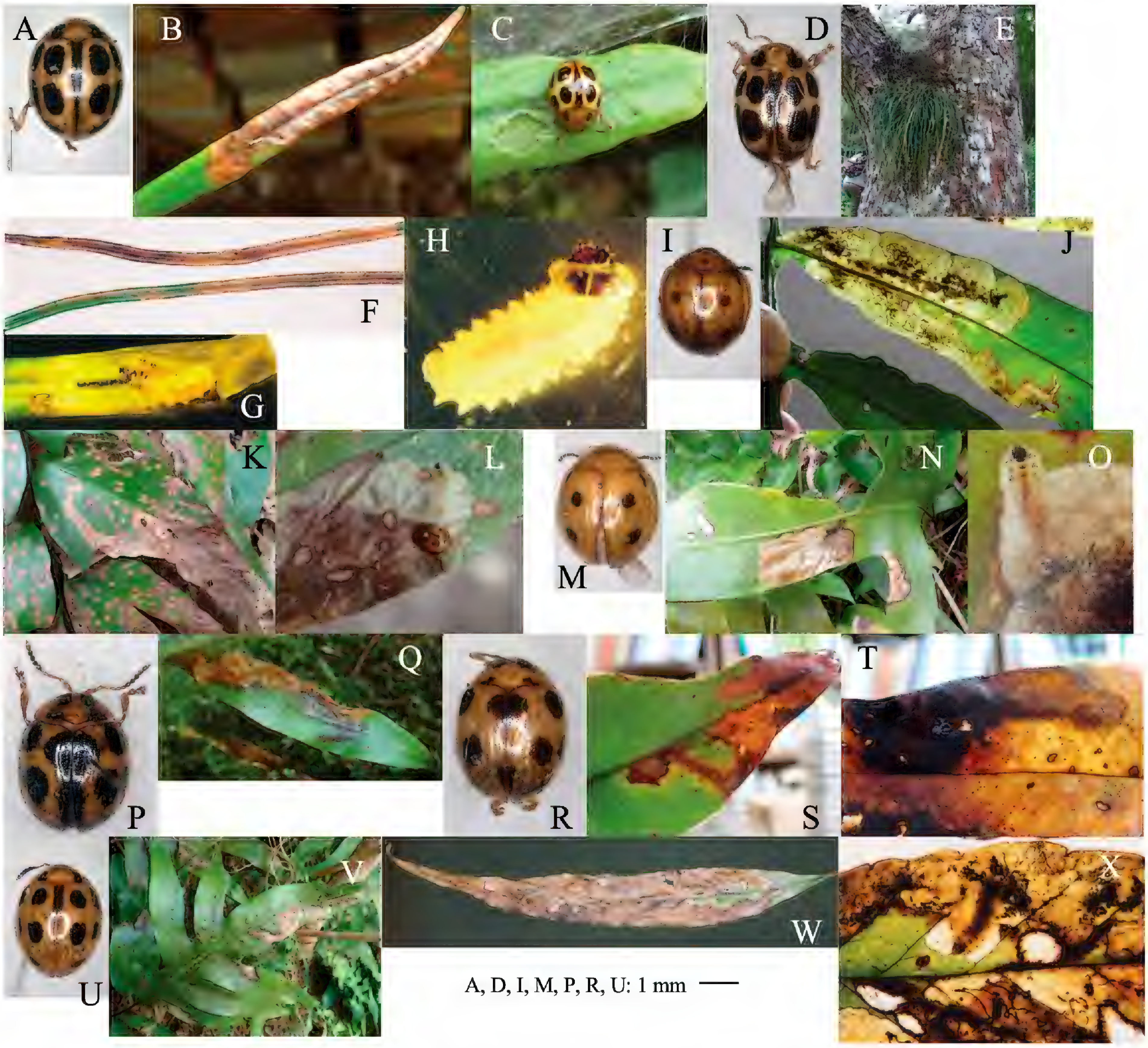

Figure 8. Habitus of adults and leaf mines of four *Halticorcus* species **A–H** *H. kasuga* **I–L** *H. sauteri* **M–T** *H. hiranoi* **U–X** *H. duodecimmaculata.* Host plants **A, B** *Lepisorus thunbergianus* at Mt. Shizuhata, Shizuoka Pref. **C** *Lepisorus onoei* at Shôjiko Lake, Yamanashi Pref. **D–H** *L. miyoshianus* at Kiso-fukushima, Nagano Pref. **I–J** *Leptochilus neopothifolius* at Kanyû, Kakeroma Is., Kagoshima Pref. **K–L** *Cyrtomium falcatum* at Imasato, Amami-ôshima Is., Kagoshima Pref. **M–O** *Phymatosorus scolopendria* at Tonaki Is., Okinawa Pref. **P, Q** *Loxogramme salicifolia* at Inohae, Kitago, Miyazaki Pref. **R–T** *Pyrrosia lingua* at Mt. Yuwan, Amami-ôshima Is., Kagoshima Pref. **U, V** *Phymatosorus scolopendria* at Iriomote Is., Okinawa Pref. **W, X** *Crypsinus yakushimensis* at Iriomote Is., Okinawa Pref.

Nephrolepis cordifolia), emerged on 2-VII-1996; • 1 adult, Naon, Yamato, Amami-ôshima Is. Kagoshima Pref., 11-V-2002 (as larva on *Colysis elliptica*), emerged on 11-VI-2002; • 10 adults, Segiri, Nagata, Yaku Is., Kumage-gun, Kagoshima Pref., 27-V-1990 (as larva on *Leptochilus neopothifolius*), emerged on ?-VII-1990; • 3 adults, Higashinamaka, Amami-ôshima Is. Kagoshima Pref., 20-V-2015 (as larva on *Leptochilus neopothifolius*), emerged on 17–18-VI-2015 (Fig. 8I–J); • 2 adults, Mt. Yuwan, Uken, Amami-ôshima Is., Kagoshima Pref., 30-VI-1992 (as larva on *Microsorum buergerianum*), emerged on 25-VII-1992; • 1 adult and several leaf mines, Tonaki Is., Shimajiri-gun, Okinawa Pref., 18-III-2020 (as larva on on *Phymatosorus scolopendria*), emerged on 20-V-2020 (Fig. 8M–O).

Halticorcus hiranoi **(Takizawa, 1982)**
Fig. 8P–T

Host plant. Aspleniaceae: *Asplenium antiquum* Makino; Polypodiaceae: *Pyrrosia lingua*, *Lemmaphyllum microphyllum*, *Lepisorus thunbergianus*, *Leptochilus neopothifolius*, *Loxogramme salicifolia*; Vittariaceae: *Vittaria flexuosa* Fee.

Leaf mine. Upper-layer linear-blotch mine on mature leaf (Fig. 8Q, S, T). Frass is thread-like, thin, and often intermittent, and deposited along meandering larval trajectory. The fully grown larva exits the mined leaf, falls to the ground, and pupates underground.

Material examined. • 1 adult and several leaf mines, Inohae, Nichinan, Miyazaki Pref., 20-V-2015 on *Loxogramme salicifolia* (Fig. 8P, Q); • 3 adults, Mt. Yuwan, Uken, Amami-ôshima Is., Kagoshima Pref., 8-III-2000 (as larva on *Pyrrosia lingua*), emerged on 14–18-V-2000 (Fig. 8R–T); • 1 adults, Mt. Yuwan, Uken, Amami-ôshima Is., Kagoshima Pref., 16-II-1999 (as larva on *Lepisorus thunbergianus*), emerged on 22-IV-1999; • 4 adult, Mt. Yuwan, Uken, Amami-ôshima Is., Kagoshima Pref., 7-III-2004 (as larva on *Asplenium antiquum*), emerged on 25-V–5-VI-2004; • 2 adults, Mt. Katsuu-dake, Nago, Okinawa Pref., 23-XII-1989 (as larva on *Lemmaphyllum microphyllum*), emerged on ?-III-1990; • 1 adult, Inokawa-dake, Tokunoshima Is., Kagoshima Pref., 12-III-2001 (as larva on *Vittaria flexuosa*), emerged on 25-VI-2001; 8 adults, Kuroshima Is., Mishima-mura, Kagoshima Pref., 11-III-1995 (as larva on *Vittaria flexuosa*), emerged on 21–25-V-1995.

Halticorcus duodecimmaculata **(S.-H. Chen, 1934)**
Fig. 8U–X

Host plant. Polypodiaceae: *Phymatosorus scolopendria*, *Selliguea yakushimensis* (Makino).

Leaf mine. Full-depth linear-blotch mine on mature leaf (Fig. 8V–X). Frass is thread-like, thin, and often intermittent, and deposited along meandering larval trajectory. The fully grown larva exits the mined leaf, falls to the ground, and pupates underground.

Material examined. • 5 adults, Ômija, Iriomote Is., Yaeyama, Okinawa Pref., 27-III-2018 (as larva on *Phymatosorus scolopendria*), emerged on 25-V–7-VI-2018 (Fig. 8U, V); • 9 adults, Urauchi, Iriomote Is., Yaeyama, Okinawa Pref., 11-V-1999 (as larva on *Selliguea yakushimensis* collected by Shirô Kobayashi), emerged on ?-VI-1999 (Fig. 8W, X).

Argopistes **Motschulsky, 1860**

Argopistes coccinelliformis **Csiki, 1940**
Fig. 9A, B

Host plant. Oleaceae: *Ligustrum micranthum* Zucc., *L. ovalifolium* Hassk. *Ligustrum japonicum* Thunb., *Osmanthus heterophyllus* (G. Don), *O. insularis* Koidz., *O.* × *fortunei* Carr. are also recorded as adult hosts (Kimoto and Takizawa 1993). In Ogasawara Islands, this is the only leaf-mining chrysomelid species.

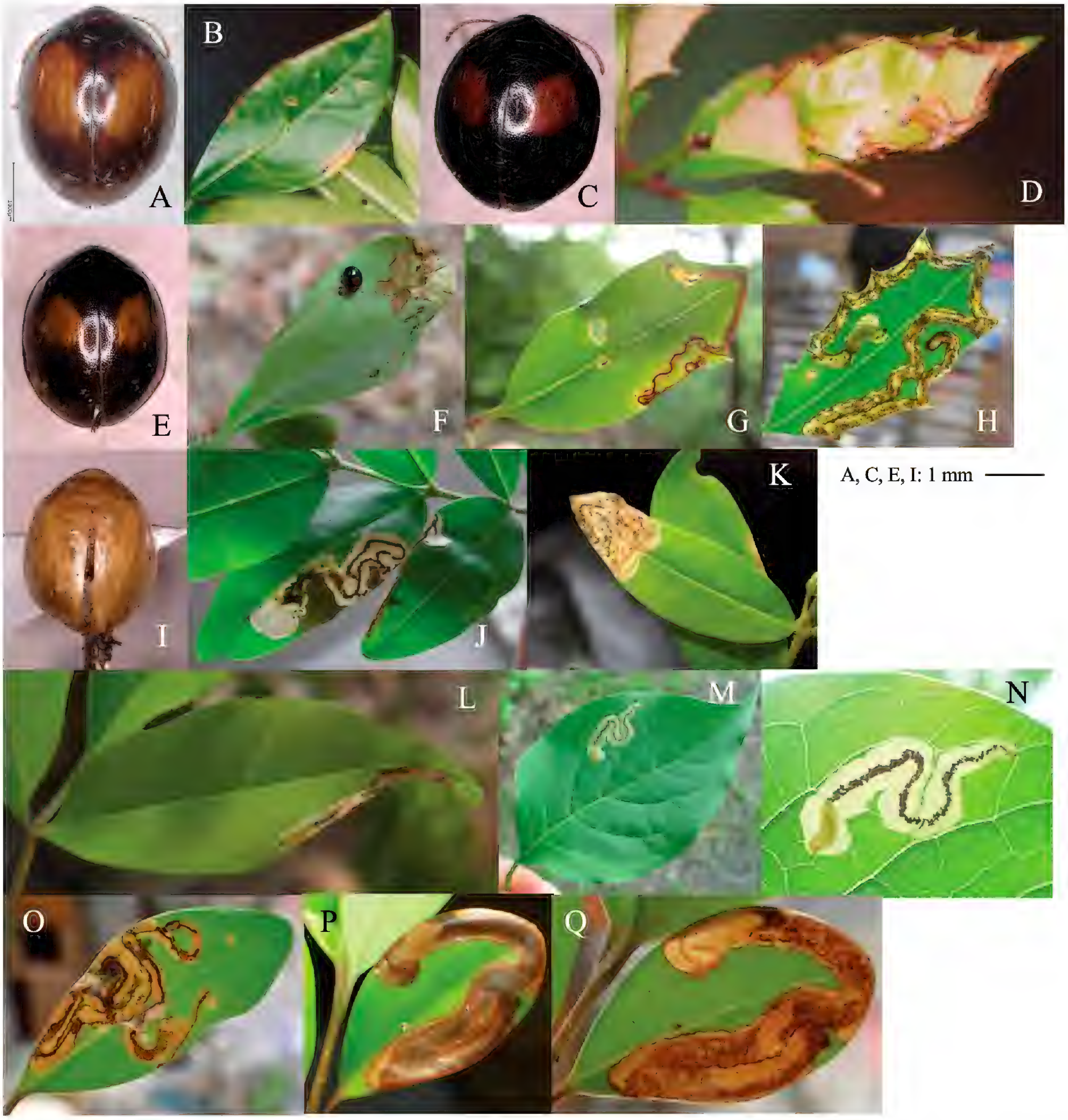

Figure 9. Habitus of adults and leaf mines of four *Argopistes* species **A, B** *A. coccinelliformis* **C–H** *A. biplagiata* **I–N** *A. tsekooni* **O–Q** *A. ryukyuensis.* Host plants **A, B** *Ligustrum ovalifoliums* at Shirahama, Wakayama Pref. **C, D** *Osmanthus × fortunei* at Mizorogaike Lake, Kyôto Pref. **E–H** *Osmanthus heterophyllus* at Iwakura, Kyôto Pref. **I–K** *Ligustrum obtusifolium* at Mt Nabejiri, Shiga Pref. **L** *Fraxinus sieboldiana* at Uri-tôge, Hamamatsu, Shizuoka Pref. **M, N** *Syringa reticulata* at Tôro Lake, Kushiro, Hokkaido **O–Q** *Ligustrum japonicum* at Abu, Okinawa Is., Okinawa Pref.

Leaf mine. Full-depth linear mine on young leaf (Fig. 9B). The egg is laid on leaf margin, and the hatched larva mines adjoining along the leaf margin or its mine. Frass is thread-like, deposited along the middle line of the mine. The fully grown larva exits the mined leaf, falls to the ground, and pupates underground.

Material examined. • 3 adults, Rinkai, Shirahama, Nishimuro-gun, Wakayama Pref., 13-V-1998 (as larva on *Ligustrum ovalifolium*), emerged on 2-VI-1998 (Fig. 9A, B); • 1 adult, Mukô-jima Is. Ogasawara, Tokyo Pref. on *Ligustrum micranthum*.

Argopistes biplagiata **Motschulsky, 1860**
Fig. 9C–H

Host plant. Oleaceae: *Ligustrum japonicum*, *Osmanthus heterophyllus*, *O. insularis*, *O.* × *fortunei*.

Leaf mine. Full-depth linear mine on young leaf (Fig. 9D, G, H). The egg is laid on the leaf margin, and the hatched larva mines adjoining along the leaf margin or its mine. Frass is thread-like, deposited along the middle line of the mine in young instars, but in old instars along meandering larval trajectory, scattered throughout the mine. The fully grown larva exits the mined leaf, falls to the ground, and pupates underground.

Material examined. • 15 adults and many leaf mines, Mizorogaike Lake, Sakyo, Kyoto Pref., 13-V-1998 on *Osmanthus* × *fortunei* (Fig. 9C, D); • 7 adults, Iwakura, Sakyo, Kyoto Pref., 13-V-2016 (as larva on *Osmanthus heterophyllus*), emerged on 4–8-VI-2016 (Fig. 9E–H).

Argopistes tsekooni **Chen, 1934**
Fig. 9I–N

Host plant. Oleaceae: *Ligustrum obtusifolium* Sieb. et Zucc., *Fraxinus sieboldiana* Blume, *Syringa reticulata* (Blume).

Leaf mine. Full-depth wide linear mine on mature leaf in young instars and full-depth ophiogenous blotch mine in old instars (Fig. 9J–N). The mine is wider than the larval width, and frass is thick thread-like, deposited linearly along the middle line of the mine. The fully grown larva exits the mined leaf, falls to the ground, and pupates underground.

Material examined. • 3 adults, Mt. Nabejiri, Taga, Shiga Pref., 23-V-2015 (as larva on *Ligustrum obtusifolium*), emerged on ?-VII-2015 (Fig. 9I–K); • 7 adults, Iwakura, Sakyo, Kyoto Pref., 22-IV-2013 (as larva on *Fraxinus sieboldiana*), emerged on 3-VI-2013 (Fig. 9L); • 7 adults, Tôro Lake, Shibecha, Kawakami-gun, Kushiro, Hokkaido, 25-VI-2017 (as larva on *Syringa reticulata*), emerged on 8-VIII-2017 (Fig. 9M, N).

Argopistes ryukyuensis **Shigetoh & Suenaga, 2022**
Fig. 9O–Q

Host plant. Oleaceae: *Ligustrum japonicum*.

Leaf mine. Full-depth wide linear mine on mature leaf in young instars and full-depth ophiogenous blotch mine in old instars (Fig. 9O–Q). Frass is thread-like, deposited along the middle line of the mine in young instars, but in old instars along meandering larval trajectory, scattered throughout the mine. The fully grown larva exits the mined leaf, falls to the ground, and pupates underground.

Material examined. Several leaf mines, Abu, Nago, Okinawa Is., Okinawa, Pref., 18-V-2017 (Fig. 9O–Q).

Argopistes unicolor Jacoby, 1885

Host plant. Oleaceae: *Osmanthus heterophyllus* (Hayashi et al. 1984; Kimoto and Takizawa 1993).

Leaf mine. Unknown.

Argopus Fischer von Waldheim, 1824

Argopus balyi Harold, 1878

Fig. 10A–D

Host plant. Ranunculaceae: *Clematis stans* Sieb. et Zucc. *C. apiifolia* DC. and *Clematis terniflora* DC. are recorded as adult hosts (Hayashi et al. 1984; Kimoto and Takizawa 1993).

Leaf mine. Upper-layer radiate mine along primary leaf vein in young instars (Fig. 10C) and full-depth blotch mine in old instars (Fig. 10D) occur on the mature leaves. Frass is thin threadlike, deposited along meandering larval trajectory in the mine. The fully grown larva exits the mine, falls to the ground, and pupates underground.

Material examined. • 1 adult, Fukuji-onsen, Takayama, Gifu Pref., 3-X-2018 (as larva on *Clematis stans*), emerged on 9-V-2018 (Fig. 10A–D); • 1 adult, Iwakura, Sakyo, Kyoto Pref., 12-X-2009 (as larva on *C. stans*), emerged on 10-V-2009.

Argopus clarki Jacoby, 1885

Host plant. Ranunculaceae: *Clematis terniflora* is recorded as larval and adult hosts (Kimoto and Takizawa 1993).

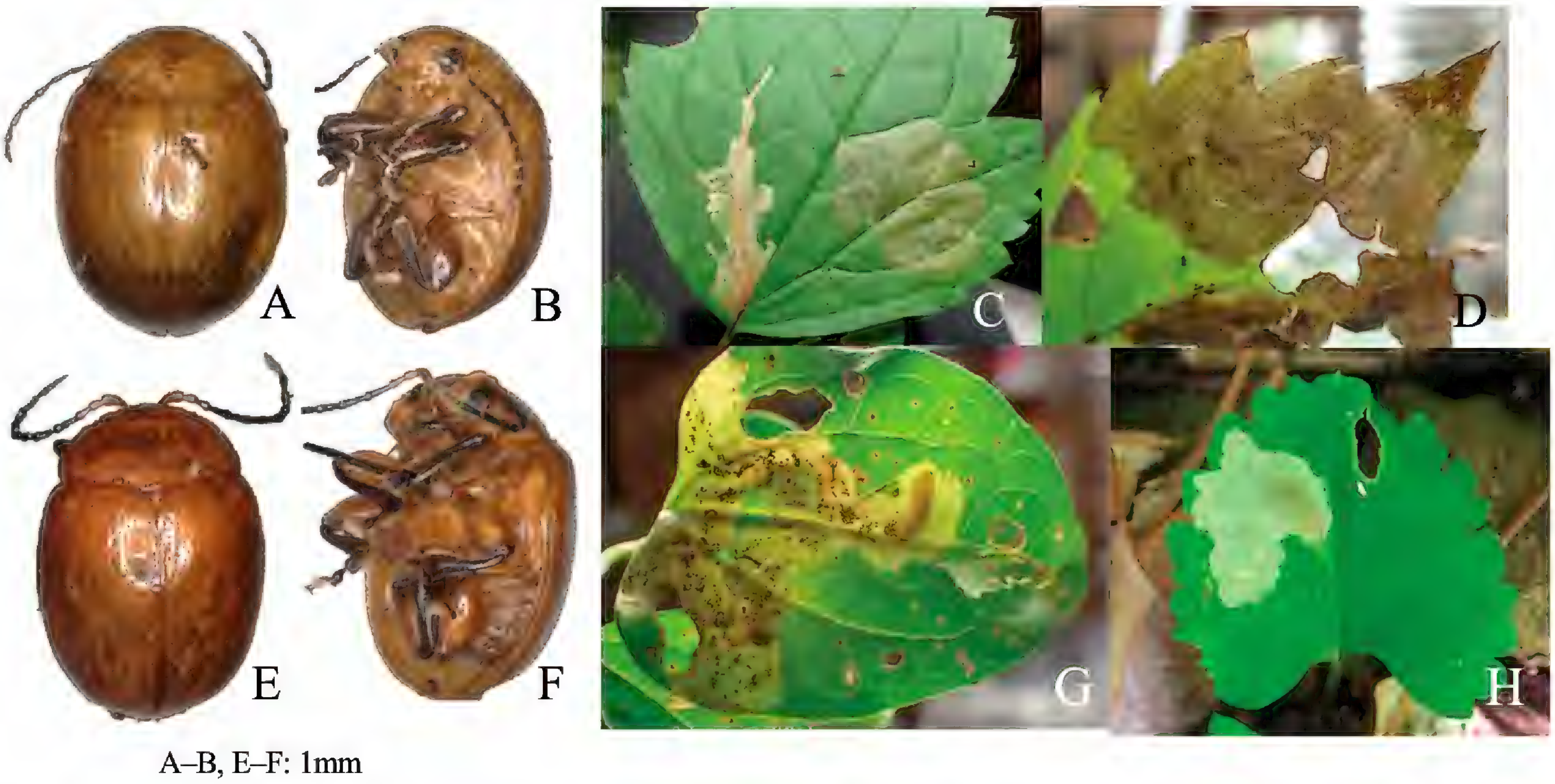

Figure 10. Habitus of adults and leaf mines of four *Argopus* species **A–D** *A. balyi* **E–H** *A. clypeatus*. Host plants **A–D** *Clematis stans* at Fukuji-onsen, Gifu Pref. **E–H** *Clematis terniflora* (**E–G** at Tsushima Nagasaki Pref., **H** at Uri-tôge, Shizuoka Pref.).

Argopus clypeatus Baly, 1874
Fig. 10E–H

Host plant. Ranunculaceae: *Clematis terniflora*, *C. apiifolia* (Hayashi et al. 1984; Kimoto and Takizawa 1993).

Leaf mine. Whitish full-depth blotch mine on mature leaf (Fig. 10G, H). Frass is granular, deposited along the larval trajectory in the mine. The fully grown larva exits the mined leaf, falls to the ground, and pupates underground.

Material examined. • 3 adults, Mine, Kami-tsusima Is., Nagasaki Pref., 19-VI-2016 (as larva on *Clematis terniflora*), emerged on 18–29-VIII-2016 (Fig. 10E–G); • 6 adults, Uri-tôge, Mikkabi, Hamamatsu, Shizuoka Pref., 22-IV-2013 (as larva on *C. terniflora*), emerged on 28-V–7-VI-2013 (Fig. 10H); • 5 adults, Nekata, Hamakita, Shizuoka Pref.

Argopus punctipennis (Motschulsky, 1866)
Fig. 11A–S

Note. Leaf-mining larvae of this species have been found from 26 plant species belonging to three taxonomically isolated plant families: Aristolochiaceae (Fig. 11A–G), Ranunculaceae (Fig. 11H–M) and Asteraceae (Fig. 11N–T). The morphology of the adult beetle (Fig. 11A, B, G–H, N–P) and its male genitalia (Fig. 11C, D, J, K, P, Q) suggest that all these specimens belong to this species.

Host plant. Aristolochiaceae: *Asarum asperum* F. Maek., *A. blumei* Duch., *A. caulescens* Maxim., *A. curvistigma* F. Maekawa, *A. heterotropoides* Miq., *A. megacalyx* (F. Maek.), *A. nipponicum* F. Maek., *A. sieboldii* Miq., *A. tohokuense* Yamaji et Ter. Nakam; Ranunculaceae: *Aconitum gigas* H. Lév. et Vaniot, *A. japonicum* Thunb., *A. okuyamae* Nakai, *A. pterocaule* Koidz., *A. sachalinense* F. Schmidt; Asteraceae: *Cirsium austrohidakaense* Kadota, *C. iito-kojianum* Kadota, *C. japonicum* Fisch. ex DC., *C. kamtschaticum* Ledeb, *C. kiotoense* (Kitam.), *C. makinoi* Kadota, *C. microspicatum* Nakai, *C. oligophyllum* (Franch. et Sav.), *C. otayae* Kitam., *C. taishakuense* Kadota, *C. ugoense* Nakai, *C. yoshinoi* Nakai.

Leaf mine. Upper-layer linear-blotch mine in young instars, and full-depth blotch mine in old instars occur on mature leaves (Fig. 11E–G, L, M, R, S). Frass is thin thread-like, deposited along meandering larval trajectory in the mine. The fully grown larva exits the mined leaf, falls to the ground, and pupates underground. The mining pattern is largely similar among leaves of the different plant species/families.

Material examined. Aristolochiaceae: • 1 adult, Samani, Hidaka, Hokkaidô, 31-V-2020 on *Asarum heterotropoides* (Fig. 11A, B); • 4 adults, Samani, Hidaka, Hokkaidô, 31-V-2020 (as larva on *Asarum heterotropoides*), emerged on 13–14-VII-2020 (Fig. 11C–E); • 1 adult, Hachimori, Happô, Yamamoto-gun, Akita Pref., 15-VI-2015 (as larva on *Asarum sieboldii*), emerged on ?-VII-2015; • 4 adults, Mt. Haguro, Tsuruoka, Yamagata Pref., 9-VII-2018 (as larva on *Asarum megacalyx*), emerged on 19-VIII–4-IX-2018 (Fig. 11G, H); • 6 adults, Mt. Yakeishi, Ôshû, Iwate Pref., 15-VII-2019 (as larva on *Asarum tohokuense*), emerged on 30-VIII-2018; • 1 adult, Mt. Kiyosumi, Kamogawa, Chiba Pref., 14-V-2008 (as larva on *Asarum nipponicum*), emerged on 20-VII-2008; • 1 adult, Warabino, Aoi-ku, Shizuoka, Shizuoka Pref., 11-V-2004 (as larva on *Asarum curvistigma*), emerged on 21-

VII-2004; • 1 adult, Mt. Gassan, Tsuruoka, Yamagata Pref., 12-VI-2019 (as larva on *Asarum sieboldii*), emerged on 16-V-2019; • 1 adult, Inogashira, Fujinomiya, Shizuoka Pref., 26-V-2002 (as larva on *Asarum caulescens*), emerged on 4-VII-2002; • 1 adult, Iwakura, Sakyo, Kyoto Pref., 24-V-1991 (as larva on *Asarum asperum*), emerged on ?-VII-1991.

Ranunculaceae: • 2 adults, Shiriya, Higashidôri, Shimokita, Aomori Pref., 16-VI-1995 (as larva on *Aconitum japonicum*), emerged on 13–14-VII-1995 (Fig. 11I–M); • 6 adults, Mt. Teine, Sapporo, Hokkaidô, 10-VII-1995 (as larva on *Aconitum yezoense*), emerged on 5-VIII-1995; • 4 adults, Monbetsu, Hidaka, Saru-gun, Hokkaidô, 5-VI-1993 on *Aconitum yezoense*; 3 adults, Mt. Obira, Shimamaki, Hokkaidô, 6-VII-2011 (as larva on *Aconitum pterocaule*, emerged on 28-VII-2011; • 5 adults, Hinoemata, Aizu-gun, Fukushima Pref., 16-VII-2023 (as larva on *Aconitum japonicum*, emerged on 17–21-VIII-2023; 5 adults, Mt. Hiuchi, Myôkô, Niigata Pref., 16-VII-2023 (as larva on *Aconitum japonicum*), emerged on 17–21-VIII-2023 (Fig. 11N); 12 adults, Funakawa, Oga, Akita Pref., 2-VI-2017 (as larva on *Aconitum japonicum*), emerged on 24–28-VII-2017; • 3 adults, Atsumi, Tsuruoka, Yamagata Pref., 2-VI-2017 (as larva on *Aconitum okuyamae*), emerged on 20-VII-2017; • 4 adults, Tokoro, Abashiri, Hokkaidô, 24-VII-2017 (as larva on *Aconitum gigas*), emerged on 3–15-IX-2017; • 1 adult, Mt. Yudono, Tsuruoka, Yamagata Pref., 28-VIII-2017 (as larva on *Aconitum pterocaule*), emerged on 15-X-2017; • 1 adult, Donden, Sado Is., Niigata Pref., 13-VII-2019 (as larva on *Aconitum japonicum*), emerged on ?-XI-2019; • 2 adults, Mt. Fuji, Fujinomiya, Shizuoka Pref., 27-VI-2001 (as larva on *Aconitum japonicum*), emerged on 9–12-VIII-2001.

Asteraceae: 14 adults, Aibetsu, Kamikawa, Hokkaidô, 26-VI-2016 (as larva on *Cirsium kamtschaticum*), emerged on 5–21-VIII-1995 (Fig. 11O–S); 4 adults, Kashiwadai, Chitose, Hokkaidô, 26-VI-2017 (as larva on *C. kamtschaticum*), emerged on 8–15-VIII-2017; 3 adults, Rebun Is., Hokkaidô, 9-VII-1995 (as larva on *C. kamtschaticum*), emerged on 10-VIII-1995; 1 adult, Tôbai, Nemuro, Hokkaidô, 23-VII-2018 (as larva on *C. iito-kojianum*), emerged on 28-VIII-2018; 2 adults, Mt. Yûbari, Yubari, Hokkaidô, 20-VII-2020 (as larva on *C. austrohidakaense*), emerged on 5–9-IX-2020; 1 adult, Shiriya, Higashidôri, Shimokita, Aomori Pref., 16-VI-2017 (as larva on *C. aomorense*), emerged on 13-VII-2017; 1 adult, Funakawa, Oga, Akita Pref., 2-VI-2017 (as larva on *C. makinoi*), emerged on ?-VII-2017; 4 adults, Mt. Haguro, Tsuruoka, Yamagata Pref., 9-VII-2018 (as larva on *C. ugoense*), emerged on 10-VIII--2018; 1 adult, Mt. Hiuchi, Myôkô, Niigata Pref., 14-VIII-2023 (as larva on *C. otayae*), emerged on 10–11-IX-2023; 1 adult, Mt. Hiuchi, Myoko, Niigata Pref., 4-V-2002 (as larva on *C. oligophyllum*), emerged on 10-VI-2002; 2 adults, Iwakura, Sakyo, Kyoto Pref., 1-V-1999 (as larva on *C. kiotoense*), emerged on 4-VI-1999; 1 adult, Mt. Kiyosumi, Chiba Pref., 14-V-2008 (as larva on *C. japonicum*), emerged on 20-VII-2008; 2 adults, Tochiu, Takashima, Shiga Pref., 6-V-1998 (as larva on *C. yoshinoi*), emerged on 7-VI-2017; 1 adult, Ippekiko Lake, Ito, Shizuoka Pref., 15-V-1999 (as larva on *C. microspicatum*), emerged on 14-VI-1999; 2 adults, Mt. Mikusa, Katô, Hyôgo Pref., 20-V-2018 (as larva on *C. japonicum*), emerged on 27–28-VI-2018; 1 adult, Yasukawa-keikoku, Tanabe, Wakayama Pref., 15-IV-2007 (as larva on *C. yoshinoi*), emerged on 16-V-2007; 8 adults, Hashirajima Is. Iwakuni, Yamaguchi Pref., 8-V-1993 (as larva on *C. japonicum*), emerged on 14–17-VI-1993.

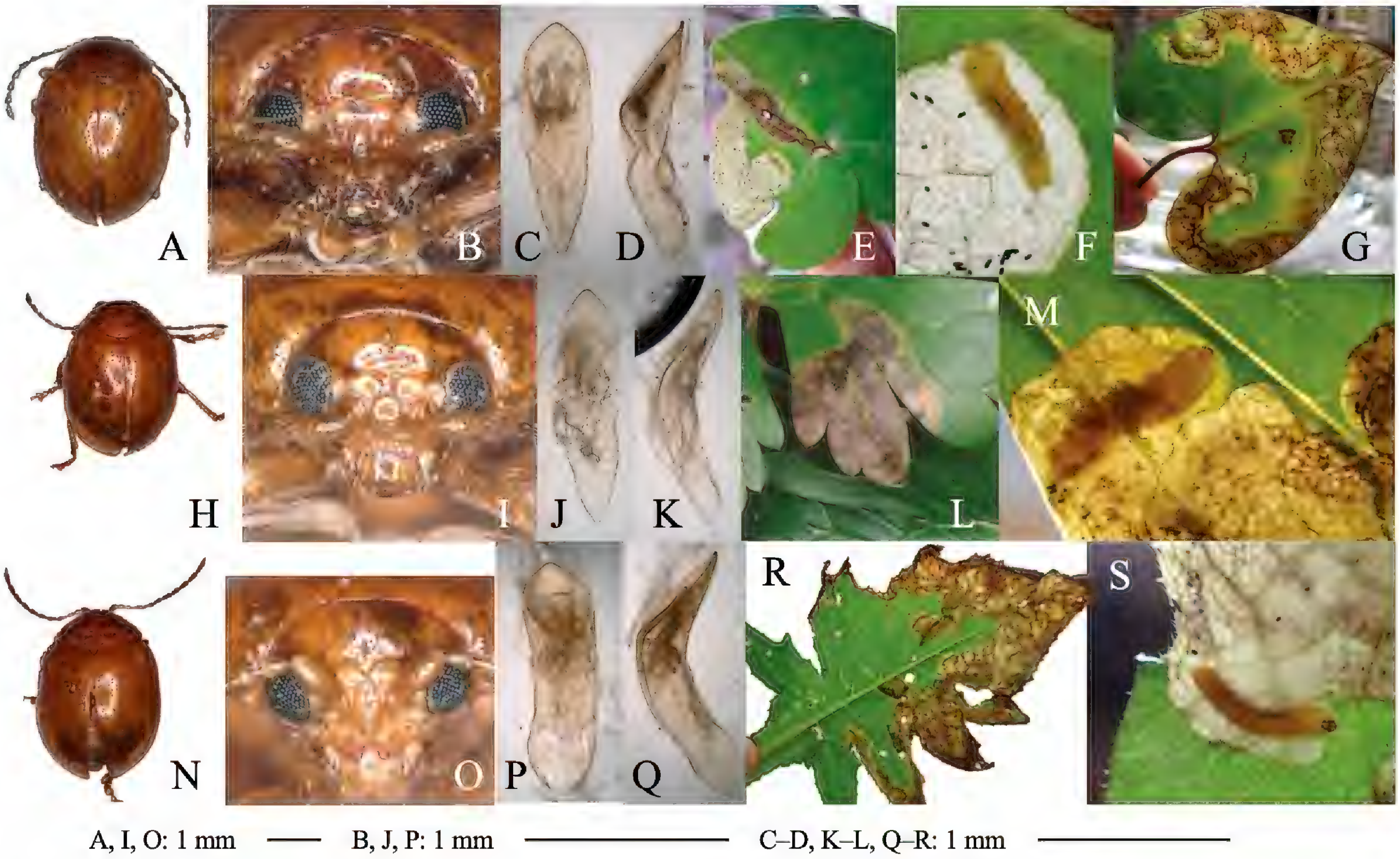

Figure 11. Adult morphology and leaf mines of *Argopus punctipennis* **A–H** on *Asarum* **I–N** on *Aconitum* **O–S** on *Cirsium*. Host plants **A–F** *Asarum heterotropoides* at Samani, Hidaka, Hokkaido **G–H** *Asarum megacalyx* at Mt. Haguro, Tsuruoka, Yamagata Pref. **I–M** *Aconitum japonicum* subsp. *subcuneatum* at Shiriya, Aomori Pref. **N** *Aconitum sachalinense* at Hinoemata, Fukushima Pref. **O–R** *Cirsium kamtschaticum* at Aibetsu, Kamikawa, Hokkaido, **S** *Cirsium japonicum* at Mt. Mikusa, Hyogo Pref. **A, I, O** Habitus **B, J, P** frontal head **C, D, K, L, Q, R** male genitalia in ventral and lateral views **E–G, L, M, R, S** leaf mines.

Argopus nigripennis (Gebler, 1823)

Note. A host plant has not been reported (Hayashi et al. 1984; Kimoto and Takizawa 1993).

Argopus unicolor Motschulsky, 1860

Note. A host plant has not been reported (Hayashi et al. 1984; Kimoto and Takizawa 1993).

Sphaeroderma Stephens, 1831

Sphaeroderma nigricolle Jacoby, 1885
Fig. 12A–O

Host plant. Liliaceae: *Cardiocrinum cordatum* (Thunb.), *Lilium auratum* Lindley, *Tricyrtis flava* Maxim, *T. macropoda* Miq.; Smilacaceae: *Smilax china* L., *S. nipponica* Miq., *S. riparia* A. DC., *S. stans* Maxim., *Heterosmilax japonica* Kunth; Stemonaceae: *Croomia heterosepala* (Baker), *C. japonica* Miq. Note: this species was collected on 11 host plants (six genera and three families of monocots, and the emerged adults varied in color and size among their host plants).

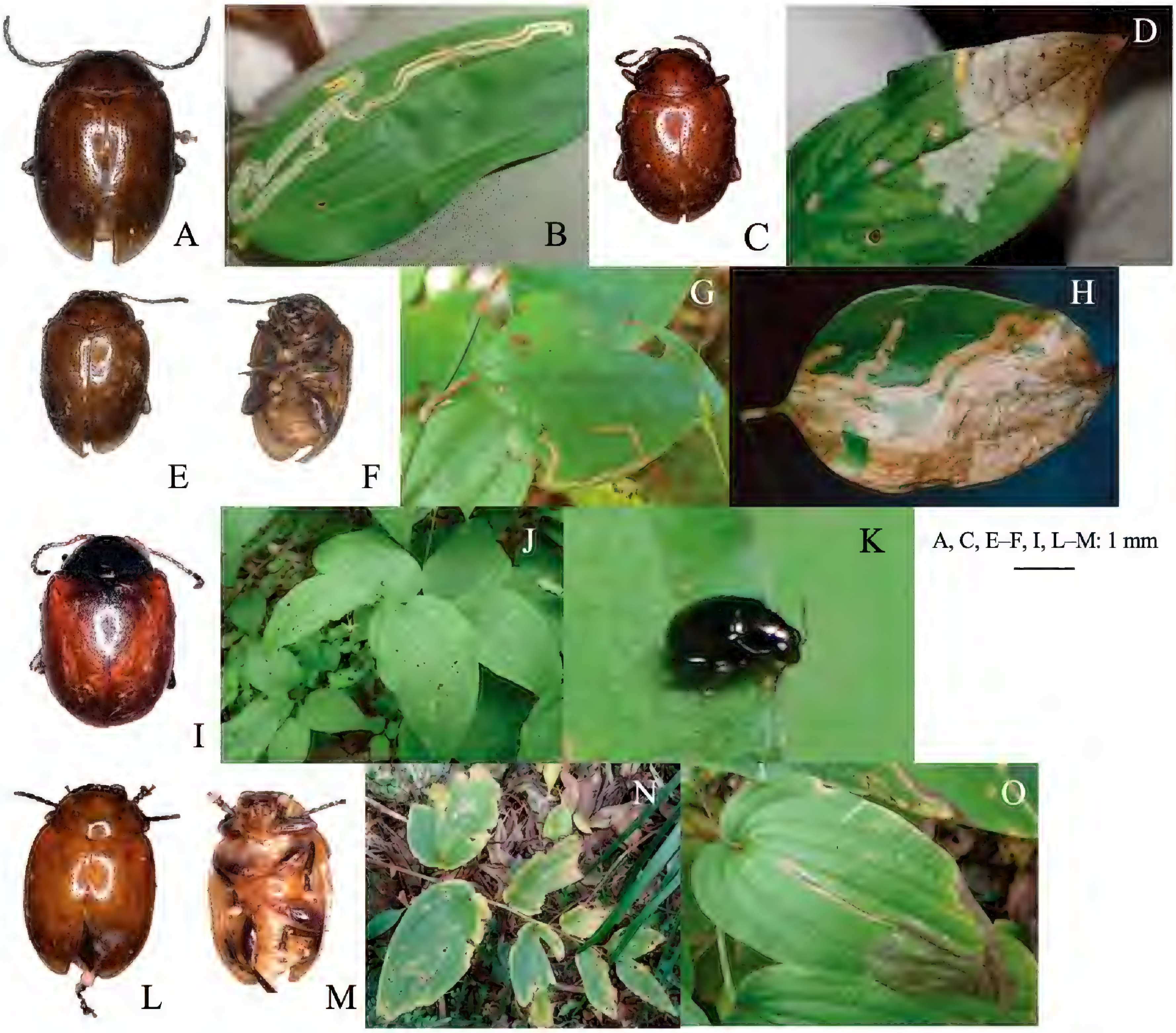

Figure 12. Habitus of adults and leaf mines of host races of *Sphaeroderma nigricolle*. Host plants **A, B** *Lilium auratum* at Mt. Haguro-san, Yamagata Pref. **C, D** *Tricyrtis macropoda* at Tengu-kogen, Kôchi Pref. **E–G** *Smilax stans* at Mt. Torigata, Kôchi Pref. **H** *Smilax stans* at Mt. Ôtaki, Kagawa Pref. **I–K** *Croomia heterosepala* at Kikuchi-keikoku, Kumamoto Pref. **L–O** *Croomia japonica* at Naon, Amami-ôshima Is., Kagoshima Pref.

Leaf mine. Full-depth long linear mine on mature leaf, often adjoining its own previous trajectory (Fig. 12B, D, G, H, J, N. O). Frass is thread-like, deposited along the middle line of the mine. The fully grown larva exits the mined leaf, falls to the ground, and pupates underground. The mine on *Tricyrtis* is unique in that the mine in young instars is not linear but radiate (Fig. 12D).

Material examined. • 5 adults, Mt. Haguro, Tsuruoka, Yamagata Pref., 8-VII-2018 (as larva on *Lilium auratum*), emerged on 31-VIII–7-IX-2018 (Fig. 12A, B); • 1 adult, Iwakura, Sakyo, Kyoto Pref., 8-IX-2008 (as larva on *Tricyrtis macropoda*), emerged on 16-XI-2008 (Fig. 12C, D); • 1 adult, Mt. Torigata, Niyodogawa, Agawa-gun, Kôchi Pref., 6-X-2020 (as larva on *Smilax stans*), emerged on 4-III-2021 (Fig. 9E–G); • 2 adults, Mt. Haguro, Tsuruoka, Yamagata Pref., 12-VI-2019 (as larva on *Smilax nipponica*), emerged on 16-VIII-2019; several leaf mines, Mt. Ôtaki, Kagawa, Pref., 7-IX-1998 on *Smilax stans* (Fig. 12H); • 1 adult, Kikuchi-keikoku, Kumamoto Pref., 2-V-2018 on *Croomia japonica* (Fig.12I–K); • 1 adult, Naon, Amami-ôshima Is., Kagoshima Pref., 12-XII-2014 (as larva on *Croomia heterosepala*), emerged on 29-VI-2015 (Fig. 12L–O).

Sphaeroderma japanum Baly, 1874
Fig. 13A–C

Host plant. Commelinaceae: *Commelina communis* L.

Leaf mine. Full-depth long linear mine on mature leaf (Fig. 13B, C). Frass is thread-like, deposited along the middle line of the mine. The fully grown larva exits the mined leaf, falls to the ground, and pupates underground.

Material examined. • 5 adults, Maki-dô, Niimi, Okayama Pref., 22-VI-2020 (as larva on *Commelina communis*), emerged on 16-III-2021 (Fig. 13A–C).

Sphaeroderma tarsatum Baly, 1874
Fig. 13D–L

Host plant. Poaceae: *Phyllostachys bambusoides* Sieb. et Zucc., *Pleioblastus chino* (Franch. et Savat.) var. *viridis* (Makino), *Sasa kurilensis* (Ruprecht), *S. nipponica* M. et S., *S. senanensis* (Franch et Savat.), *Sasamorpha borealis* (Hack.), *Shibataea kumasaca* Makino, *Stipa coreana* Honda var. *kengii* Ohwi).

Leaf mine. Upper-layer long linear mine on mature leaf, often adjoining its own trajectory (Fig. 13E–G, I, L). The egg is laid in leaf blade, hatched larva mines usually toward leaf apex along leaf vein, and sometimes turns adjoining its past mine. Frass is granular, deposited linearly along the middle line of the mine. The mining larva is found in autumn from October to December. The fully grown larva exits the mined leaf from late autumn to early winter, falls to the ground, and pupates underground. Pupa hibernates under the ground, and the adult emerges the next spring.

Material examined. • 2 adults, Akiu, Taihaku-ku, Sendai, Miyagi Pref., 14-XI-2014 (as larva on *Sasa nipponica*), emerged on 7-V-2015 (Fig. 13D–G); • 1 adult, Azusagawa, Matsumoto, Nagano Pref., 24-X-2020 (as larva on *Sasa senanensis*), emerged on 2-III-2021 (Fig. 13H, I); • 1 adult, Ashiu, Nantan, Kyoto Pref., 9-XI-1999 (as larva on *Sasa kurilensis*), emerged on 28-III-2000; 1 adult, Kuchi-sakamoto, Aoi-ku, Shizuoka, Shizuoka Pref., 27-XII-2005 (as larva on *Sasamorpha borealis*), emerged on 1-III-2006; • 1 adult, Inogashira, Fujinomiya, Shizuoka Pref., 11-XI-2001 (as larva on *Phyllostachys bambusoides*), emerged on 14-V-2002; • 3 adult, Usuzuka, Mt. Fuji, Fujinomiya, Shizuoka Pref., 24-X-2019 (as larva on *Stipa coreana* var. *kengii*), emerged on 7–10-IV-2020 (Fig. 13J–L).

Sphaeroderma seriatum Baly, 1874
Fig. 13M–P

Host plant. Poaceae: *Panicum bisulcatum* Thunb.

Leaf mine. Full-depth linear mine on mature leaf (Fig. 13N–P). The egg is laid along the leaf margin, and the hatched larva mines usually toward leaf apex along leaf margin, and sometimes turns adjoining its mine. Frass is intermittent thread-like, deposited linearly in two rows along both sides of the mine. Mining larva is found in October. The fully grown larva exits the mined leaf from late autumn to early winter, falls to the ground, pupates underground, and the adult emerges in late autumn.

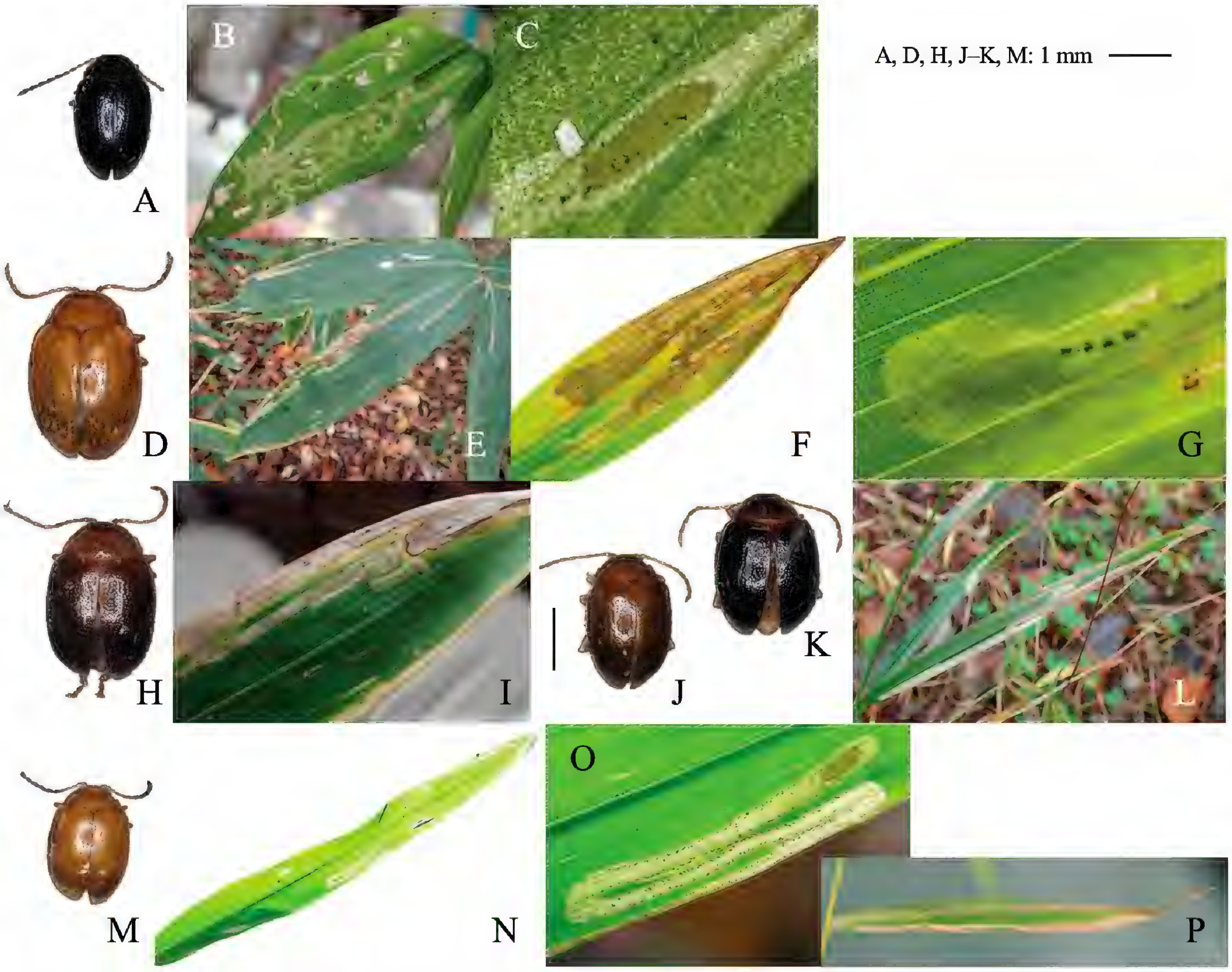

Figure 13. Habitus of adults and leaf mines of monocot-associated *Sphaeroderma* species **A–C** *S. japanum* **D–L** *S. tarsatum* **M–P** *S. seriatum*. Host plants **A–C** *Commelina communis* at Makidô, Niimi, Okayama Pref. **E–G** *Sasa nipponica* at Akiu, Sendai, Miyagi Pref. **H, I** *Sasa senanensis* at Kamikôchi, Nagano Pref. **J–L** *Stipa coreana* var. *japonica* at Mt. Fuji, Shizuoka **M–P** *Panicum bisulcatum* at Yogo Lake, Shiga Pref. (**M–O**) and at Seryo, Kyôto Pref. (**P**).

Material examined. • 3 adults, Yogo Lake, Nagahama, Shiga Pref., 12-IX-2015 (as larva on *Panicum bisulcatum*), emerged on 7-X-2015 (Fig. 13M–O); • 4 adults, Seryô, Sakyô, Kyoto, Kyoto Pref., 11-IX-1998 (as larva on *Panicum bisulcatum*), emerged on 28-IX–1-X-1998 (Fig. 13P).

Sphaeroderma apicale Baly, 1874

Host plant. Poaceae: *Miscanthus sinensis* (Hayashi et al. 1984; Kimoto and Takizawa 1993).

Leaf mine. Unknown.

Sphaeroderma akebia Ohno, 1964

Fig. 14A–C

Host plant. Lardizabalaceae: *Akebia trifoliata* (Thunb.), *A. quinata* Decne.

Leaf mine. Upper-layer linear mine on mature leaf (Fig. 14B, C). The mine is wider than the larval width, having dead ends and branches. Frass is granular

and minute, deposited linearly in two rows along both sides of the mine, and inner space between the frass lines is colored darker against the outer space. The mining larva is found from late autumn to early winter. The fully grown larva exits the mined leaf in early winter, falls to the ground, and pupates underground. The pupa hibernates underground, and the adult emerges the next spring.

Material examined. • 3 adults, Shimoike Lake, Tsuruoka, Yamagata Pref., 15-XI-2014 (as larva on *Akebia trifoliata*), emerged on 7-V-2015 (Fig. 14A–C); • 2 adults, Aibano, Takashima, Shiga Pref., 13-XII-1998 (as larva on *Akebia trifoliata*), emerged on 8-IV-1999.

Sphaeroderma inaizumii Takizawa, 2015

Fig. 14D

Host plant. Lardizabalaceae: *Akebia trifoliata*, *A. quinata.*

Leaf mine. Upper-layer blotch mine on mature leaf (Fig. 14D). The mine is orbicular, and the larva often relocates its mine. Frass is minute and often liquid, deposited as dark band in the mine. The mining larva is found from late autumn to early winter. The fully grown larva exits the mined leaf in early winter, falls to the ground, and pupates underground.

Material examined. Many leaf mines, Shoji Lake, Kawaguchiko, Yamanashi Pref., 24-XI-2018 on *Akebia trifoliata* (Fig. 14D).

Sphaeroderma quadrimaculatum Chûjô, 1935

Fig. 14E–L

Host plant. Ranunculaceae: *Clematis taiwaniana* Hayata var. *ryukiuensis* Tamura.

Leaf mine. Full-depth linear mine on mature leaf (Fig. 14F–H, L). Frass is granular and minute, deposited linearly in two rows along both sides of the mine. The fully grown larva exits the mined leaf in early winter, falls to the ground, and pupates underground.

Material examined. • 2 adults, Hedo, Kunigami, Okinawa Pref., 10-XI-2021 on *Clematis taiwaniana* var. *ryukiuensis* (Fig. 14E); • 3 adults, Hedo, Kunigami, Okinawa Pref., 14-X-2000 (as larva on *C. taiwaniana* var. *ryukiuensis*), emerged on 21-XI–10-XII-2000 (Fig. 14F–H); • 2 adults, Tonaki Is., Shimajiri-gun, Okinawa Pref., 18-III-2020 (as larva on *C. taiwaniana* var. *ryukiuensis*), emerged on 10-V-2020 (Fig. 14I–L).

Sphaeroderma flavonotatum Chûjô, 1937

Fig. 14M–Q

Host plant. Ranunculaceae: *Clematis tashiroi* Maxim. The host plant record of *Smilax* spp. by Takizawa (2021) is uncertain.

Leaf mine. Full-depth linear mine on mature leaf (Fig. 14N–P). Frass is granular, deposited as a band along middle line of the mine. The fully grown larva (Fig. 14Q) exits the mined leaf in early winter, falls to the ground, and pupates underground.

Material examined. • 6 adults, Funaura, Iriomote Is., Yaeyama, Okinawa Pref., 6-III-2019 (as larva on *Clematis tashiroi*), emerged on 20-IV-2019 (Fig. 14M–Q).

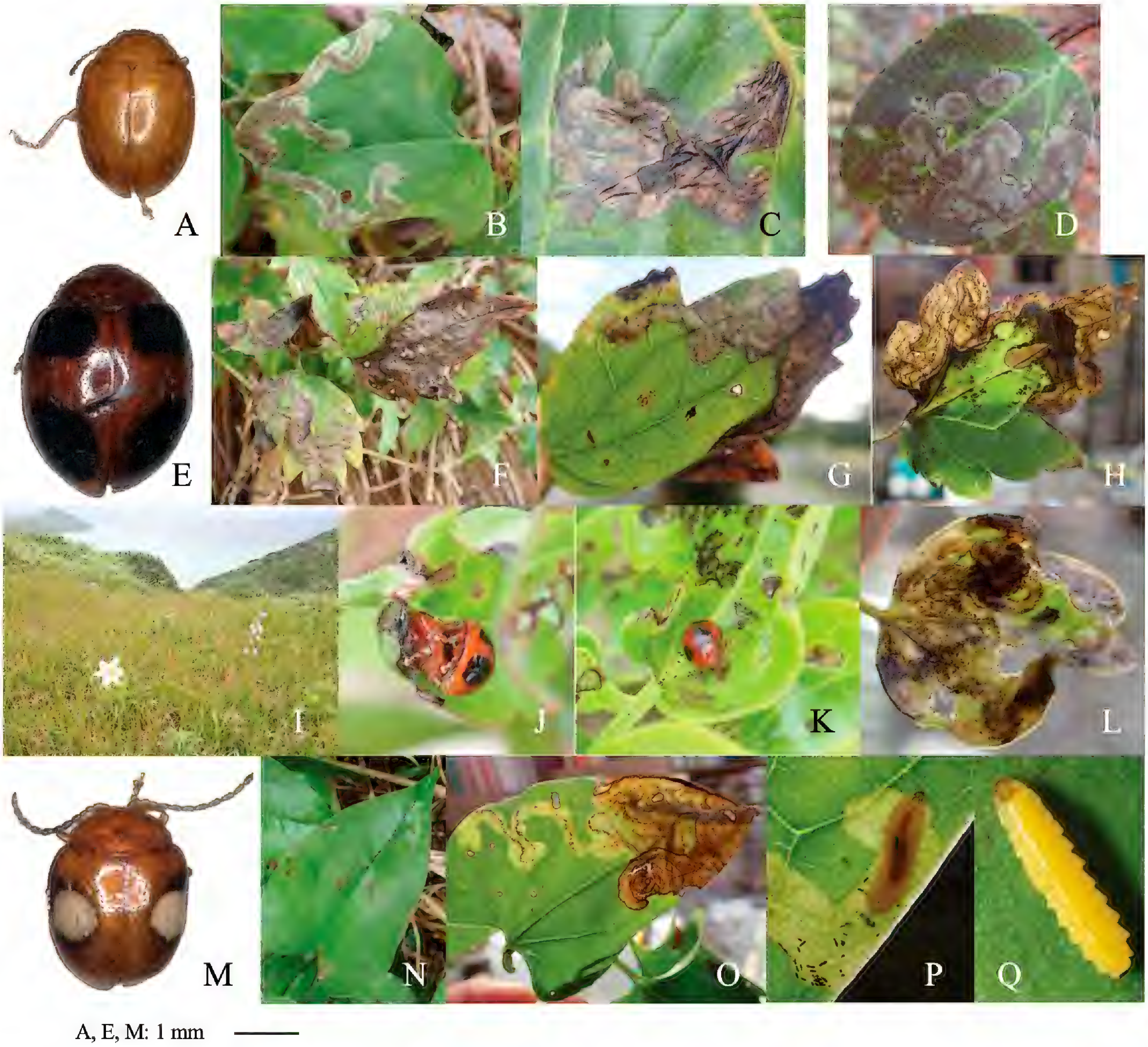

Figure 14. Habitus of adults, habitats, and leaf mines of *Akebia*-associated and *Clematis*-associated *Sphaeroderma* species **A–C** *S. akebia* **D** *S. inaizumii* **E–L** *S. quadrimaculatum* **M–Q** *S. flavonotatum* **R–V** *S. separatum*. Host plants **A–C** *Akebia trifoliata* at Tsuruoka, Yamagata Pref. **D** *Akebia trifoliata* at Shôji Lake, Yamanashi Pref. **E–G** *Clematis taiwaniana* var. *ryukiuensis* at Hedo, Okinawa Is., Okinawa Pref. **J–L** *Clematis taiwaniana* var. *ryukiuensis* at Tonaki Is., Okinawa Pref. **M–P** *Clematis tashiroi* at Iriomote Is. Okinawa Pref. **S–V** *Clematis japonica* at Shirakawa-gô, Gifu Pref.

***Sphaeroderma separatum* Baly, 1874**
Fig. 14R–V

Host plant. Ranunculaceae: *Clematis japonica*. Takizawa (2021) lists up three host plants: *C. apiifolia* DC., *C. pierotti* Miq. and *Chelidonium majus* L. (Papaveraceae).

Leaf mine. Full-depth radiate mine along leaf vein on mature leaf (Fig. 14T–V). Frass is liquefied, deposited near the center of the mine.

Material examined. • 2 adults copulating on a leaf of *Clematis japonica* at Shirakawa-gô, Shirakawa, Ôno-gun, Gifu Pref., 12-VIII-2024 (Fig. 14R, S), and many leaf mines on the plant species at the same locality 29-IX-2023 (Fig. 14T–V).

Sphaeroderma placidum **Harold, 1877**

Fig. 15A–G

Host plant. Ranunculaceae: *Clematis apiifolia*.

Leaf mine. Black upper-layer blotch mine on mature leaf. Frass is granular scattered along larval trajectory at young instars, and accumulated in a discoid area in a center of the mine in old instars. The mining larva is found from late autumn to early winter. The fully grown larva exits the mined leaf in early winter, falls to the ground, and pupates underground. The pupa hibernates under the ground, and the adult emerges the next spring.

Material examined. • 3 adults, Shoji Lake, Kawaguchiko, Yamanashi Pref., 24-XI-2018 (as larva on *Clematis apiifolia*), emerged on 10-V-2019 (Fig. 15A–D); • 2 adults, Kisofukushima, Kiso, Nagano Pref., 24-X-1999 (as larva on *Clematis apiifolia*), emerged on 22-V-2000; 11 adults and several leaf mines, Fukasawa, Gotenba, Shizuoka Pref., 29-VI-2014 on *Clematis apiifolia*; • 1 adult and several leaf mines on *Clematis apiifolia*, Ashiu, Nantan, Kyôto Pref., 13-IX-1993 (Fig. 15E–G).

Sphaeroderma unicolor **Kimoto, 1965**

Fig. 15H–L

Host plant. Ranunculaceae: *Clematis terniflora* DC., *C. apiifolia* DC.

Leaf mine. Full-depth linear mine on mature leaf, often adjoining its own trajectory (Fig. 15L). Frass is linear thread-like, deposited along a side line of the mine. Mining larva is found from late autumn to early winter. The fully grown larva exits the mined leaf in early winter, falls to the ground, and pupates underground. The pupa hibernates under the ground, and the adult emerges the next spring.

Material examined. • 1 adult and several leaf mines, Iya, Miyoshi, Tokushima Pref., 13-VI-2017 on *Clematis apiifolia* (Fig. 15J–L); • 5 adults, Aidani, Iwade, Wakayama Pref., 19-I-2002 (as larva on *Clematis terniflora*), emerged on 28-III–1-IV-2002; • 1 adult, Inogashira, Fujinomiya, Shizuoka Pref., 11-XI-1999 (as larva on *Clematis terniflora* collected by T. Kato), emerged on 14-V-2000; • 4 adults, Obama, Fukui Pref., 13-XII-1998 (as larva on *Clematis terniflora*) emerged on 4–8-IV-1998 (Fig. 15H, I).

Sphaeroderma uenoi **Takizawa, 2021**

Fig. 15M–R

Host plant. Ranunculaceae: *Clematis apiifolia*, *Clematis terniflora*.

Leaf mine. Full-depth linear mine on mature leaf (Fig. 15R). Frass is linear thread-like but intermittent. The fully grown larva exits the mined leaf in early winter, falls to the ground, and pupates underground. The pupa hibernates under the ground, and the adult emerges the next spring.

Material examined. • 2 adults and several leaf mines on *Clematis terniflora*, Kizu-gawa, Kusauchi, Kyôtanabe, Kyoto Pref., 11-X-2022 (Fig. 15M–Q); many leaf mines on *Clematis terniflora*, Iwakura, Sakyo, Kyoto Pref., 20-XII-2023 (Fig. 15R).

Figure 15. Adult morphology, behavior, and leaf mines of *Clematis*-associated and *Cimicifuga*-associated *Sphaeroderma* species **A–G** *S. placidum* **H–L** *S. unicolor* **M–R** *S. uenoi* **S–Z** *S. ohkuboi* **A, E, H, J, M, S, Y** adult habitus in dorsal view **F, N** ventral view **B, F, I, O** Frontal view of head **K, P, T** adult feeding behavior **C, D, G, L, Q, R, U–X, Z** leaf mines. Host plants **A–D** *Clematis apiifolia* at Shyôji Lake, Yamanashi Pref. **E–G** *Clematis apiifolia* at Ashiu, Kyôto Pref. **H, I** *Clematis terniflora* at Obama, Fukui Prefecture **J–L** *Clematis terniflora* at Iya, Tokushima Prefecture **M–Q** *Clematis terniflora* at Kizu-gawa, Kyôto Pref. **R** *Clematis terniflora* at Iwakura, Kyôto Pref. **S–X** *Cimicifuga japonica* at Mt. Nakatsu-myôjin, Kôchi Pref. **Y, Z** *Cimicifuga simplex* at Shirahone-onsen, Nagano Pref.

Sphaeroderma ohkuboi Chûjô, 1940

Fig. 15S–Z

Host plant. Ranunculaceae: *Cimicifuga japonica* (Thunb.), *C. biternata* (Siebold et Zucc.), *C. simplex* Wormsk.

Leaf mine. Full-depth linear mine on the mature leaf (Fig. 15V–X, Z). Frass is dark pasty, deposited as a wide band along middle line of the mine. The fully grown larva exits the mined leaf in autumn, falls to the ground, and pupates underground. The pupa hibernates under the ground, and the adult emerges the next spring.

Material examined. • 1 adult and several leaf mines, Mt. Nakatsu-myôjin, Niyodogawa, Kôchi Pref., 6-X-2020 on *Cimicifuga japonica* (Fig. 15S–X); 1 adult, Shirahone, Matsumoto, Nagano Pref., 15-X-2013 (as larva on *C. simplex*), emerged on ?-V-2014 (Fig. 15Y, Z); • 1 adult, Toyohara, Nasu, Tochigi Pref., 14-IX-2003 (as larva on *C. simplex*), emerged on 3-V-2004.

Sphaeroderma balyi Jacoby, 1885

Fig. 16A–J

Host plant. Asteraceae: *Farfugium japonicum* (L.), *Parasenecio kamtschaticus* (Maxim.), *P. amagiensis* (Kitam.), *P. yatabei* (Matsum. et Koidz.), *Petasites japonicus* (Siebold et Zucc.).

Leaf mine. Upper-layer linear mine on the mature leaf, with trajectories usually adjoining each other (Fig. 16B, E, I, J). Frass is minute granular, deposited linearly along either side of the mine. The fully grown larva exits the mined leaf in autumn, falls to the ground, and pupates underground.

Material examined. • 2 adults, Mt. Teine, Sapporo, Hokkaidô, 10-VII-1995 (as larva on *Petasites japonicus*), emerged on 10-VIII-1995; • 1 adult, Shimoike, Tsuruoka, Yamagata Pref., 12-VI-2019 (as larva on *Petasites japonicus*), emerged on 10-VII-2019; • 1 adult, Mt. Haguro, Tsuruoka, Yamagata Pref., 8-VII-2018 (as larva on *Petasites japonicus*), emerged on ?-IV-2019; 1 adult, Renge-onsen, Itoigawa, Niigata Pref., 1-VII-2013 (as larva on *Petasites japonicus*), emerged on 10-VIII-2013; • 4 adults, Ukawa, Kyôtango, Kyoto Pref., 17-IX-2019 (as larva on *Petasites japonicus*), emerged on 15–20-X-2019 (Fig. 16A–C); • 1 adult, Nagawado, Matsumoto, Nagano Pref., 12-VII-2003 (as larva on *Petasites japonicus*), emerged on 1-IX-2003; • 2 adults, Tôbai, Nemuro, Hokkaidô, 23-VII-2018 (as larva on *Parasenecio kamtschaticus*), emerged on 30-VII–4-VIII-2018 (Fig. 16D, E); • 1 adult, Torikura-rindo, Ôshika, Nagano Pref., 30-VI-2013 (as larva on *Parasenecio yatabei*), emerged on 28-VIII-2013; • 1 adult, Yawatano, Izu, Shizuoka Pref., 12-V-2002 (as larva on *Parasenecio amagiensis* collected by T. Kato), emerged on 26-VI-2002; • 3 adults, Amatsu-kominato, Kamogawa, Chiba Pref., 14-V-2008 (as larva on *Farfugium japonicum*), emerged on 27-V-2008; 3 Dôgashima, Nishiizu, Shizuoka Pref., 9-V-2004 (as larva on *Farfugium japonicum*), emerged on 23-VI-2004; 3 Ena, Yura, Hidaka-gun, Wakayama Pref., 19-V-2002 (as larva on *Farfugium japonicum*), emerged on 12–15-VI-2002; • 2 adults, Ashizuri-misaki, Tosashimizu, Kochi Pref., 23-IV-2018 (as larva on *Farfugium japonicum*), emerged on 7-VI-2018; • 1 adult and manly leaf mines, Kobukei, Nichinan, Miyazaki Pref., 23-X-2022 on *Farfugium japonicum* (Fig. 16F–J).

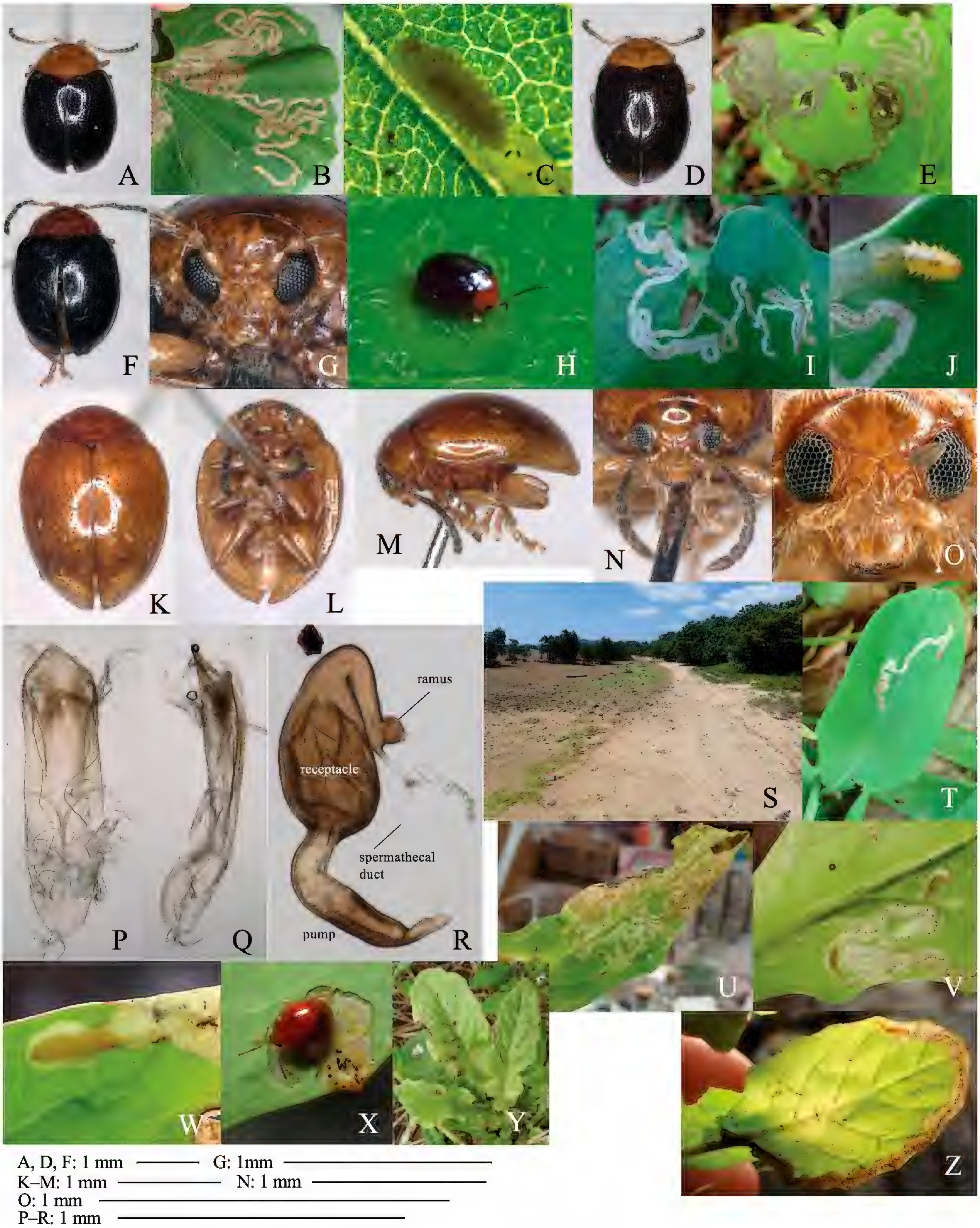

Figure 16. Adult morphology, behavior, and leaf mines of Asteraceae-associated *Sphaeroderma* species **A–J** *S. balyi* **K–Z** *S. komiana* sp. nov. **A, D, F** adult habitus in dorsal view **G, O** frontal view of head **H, X** adult feeding behavior **L–N** ventral, lateral, frontal view **P–Q** male genitalia **R** female spermatheca **S** landscape of the habitat at type locality **B, C, E, I, J, T–W, Y, Z** leaf mines. Host plants **A–C** *Petasites japonicus* at Ukawa, Kyôtango, Kyôto Pref. **D, E** *Parasenecio kamtschaticus* at Tôbai, Nemuro, Hokkaido **F–J** *Farfugium japonicum* at Kobukei, Nichinan, Miyazaki Pref. **T–X** *Ixeris japoica* at Komi, Iriomote Island, Okinawa Pref. **Y–Z** *Youngia japonica* at Hoshidate, Iriomote Is., Okinawa Pref.

Sphaeroderma fulvoapicale **Kimoto & Gressitt, 1966**

Host plant. Asteraceae: *Farfugium japonicum* (L.) (Takizawa, 2021).

Leaf mine. Unknown.

Sphaeroderma komiana **Kato, sp. nov.**

https://zoobank.org/390A08F4-3F79-4548-8F94-409EA1A23E5A

Fig. 16K–Z

Type locality. Japan: Okinawa Pref., Iriomote Is., Komi.

Type material. ***Holotype***: • ♂, Komi, Iriomote Is., Yaeyama, Okinawa Pref. (24.319°N, 123.910°E, 4 m above sea level), 16-III-2018 (collected as larva on *Ixeris japonica* by M. Kato), emerged on 15-V-2018 (NSMT-I-C- 200350). ***Paratypes***: • 3 ♂ 1 ♀, same data with holotype, emerged on 11–15-V-2018 (NSMT-I-C- 200351–200354); • 3 ♂ 2 ♀, Shirahama, Iriomote Is., Yaeyama, Okinawa Pref., 16-III-1999 (as larva on *Lactuca indica*), emerged on 21–25-IV-1999 (NSMT-I-C-200355– 200359).

Diagnosis. The species is a small oblong-oval, strongly convex beetle (length 1.8–1.9 mm) with a shiny, completely reddish brown body, elytra, and legs. The head features a pair of distinctly delimited frontal tubercles that contact each other at postero-inner angles. The inter-antennal area is raised and fusiform. The male genitalia exhibit a laterally uncurved aedeagus. The larva mines the leaves of Asteraceae plants including *Ixeris japonica*, *Lactuca indica*, and *Youngia japonica*.

Description. Adult male (Fig. 16K–Q). ***Habitus.*** The body is oblong-oval and strongly convex on the dorsal side, measuring 1.8–1.9 mm in length (Fig. 16K, N). It is reddish brown, with black eyes. The antennae are dark brown, and the four basal segments, pronotum, and elytra are reddish brown (Fig. 16N).

Head. The head has a smooth, shiny, impunctate vertex. The frontal tubercles are transverse and posteriorly delimited by a nearly straight, deep, sharp sulcus, with antero-inner and antero-outer angles produced below, well-delimited behind by a sharp furrow, almost contacting each other at postero-inner angles (Fig. 16O). The inter-antennal area is raised and fusiform, with the diameter of the raised area narrower than that of the antennal socket. The eyes are strongly convex, with their transverse diameter in frontal view being 0.8-fold wider than the inter-ocular distance. The clypeus has an entire anterior fringe. The antennae are half as long as the body. The proportional lengths of antennomeres 1–11 are as follows: 1:0.50:0.38:0.51:0.65:0.65:0.65:0.65:0.69:0.69:0.91.

Thorax. The pronotum is transverse, 1.7-fold as wide as long, with the widest point located slightly before basal angles, and broadly arched at the posterior margin, with roundly produced anterior angles. The disc is evenly convex, sparsely covered with small punctures and interspaced with smooth and shining areas. The scutellum is rounded and triangular in shape, flat, impunctate, and as long as wide. The elytra are oblong and strongly convex, each measuring 2.1-fold as long as wide, widest at the basal one-fourth area and then rounded and narrowed toward the apex (Fig. 16K). The disc is densely covered with 11 partially irregular, longitudinal striae of small punctures. The epipleura are wide at the base, with gradual narrowing and disappearance

before the apex. The epipleural disc is impunctate and smooth. The prosternum is narrow with a stout longitudinal carina as wide as the length of the 10th antennal segment (Fig. 16L).

Abdomen. The fifth visible abdominal sternite is densely covered with punctures bearing long hairs and is weakly concave apically, with a dark median longitudinal line. The legs are stout, with the first tarsal segments being moderately enlarged but distinctly narrower than the third segment. The hind legs have significantly enlarged femora.

Genitalia. (Fig. 16P, Q) The aedeagus is lanceolate in dorsal view, 3.6-fold longer than its width, almost parallel-sided, and narrowed to a rounded triangular apex. Slightly curved in lateral view, with the ventral surface almost flat. The ostium is membranous, containing an inverted V-shaped sclerotized area.

Female. The body is slightly enlarged, ~ 2.0–2.2 mm in length.

Genitalia. (Fig. 16R) The spermatheca is brown and sclerotized, consisting of a proximal swollen receptacle and a distal strongly curved slender pump, with the apex attenuated and curved inward. The receptacle and pump exhibit many transverse wrinkles. The spermathecal duct is proximally sclerotized, connecting to a thin transparent duct. The distal portion of the sclerotized spermathecal duct carries a globular ramus.

Distribution. The only known distribution is on Iriomote Island, Japan.

Host plant. Asteraceae: *Ixeris japonica* (Burm. f.) (Fig. 16T–X), *Lactuca indica* L., *Youngia japonica* (L.) (Fig. 16Y, Z). *Ixeris japonica* grows on sandy beaches along coral reefs and mangroves (Fig. 16S). *Lactuca indica* and *Y. japonica* grow along margins of rice field paddies.

Leaf mine. Full depth linear mines on mature leaf, without crossing, backtracking, or branching (Fig. 16T–W, Y, Z). Typically, the mine is initiated near the midrib, seldom adjoining other mines. Minute granular frass is linearly deposited along the subcentral line of the mine. Upon reaching maturity, the larva exits the mined leaf in autumn and drops to the ground, where it pupates beneath the soil surface.

Etymology. The species name refers to the village name of the type locality, which is also the original name of Iriomote Island (Komi).

Japanese name. Komi-tamanomi-hamushi.

Remarks. This newly identified species resembles asterid-associated *S. balyi* in terms of size, habitus, punctuation of elytra, and frontal tubercles of the head. However, it is distinctly differentiated from the latter by the reddish-brown color of the elytra (black in *S. balyi*), parallel-sided and dorso-ventrally flattened aedeagus (aedeagus in the latter having lateral constriction in the middle and strongly curved in lateral view; Kimoto and Takizawa 1993: pl. 84, fig. 9), host plant genera (*Ixeris*, *Lactuca*, and *Youngia* vs *Farfugium*, *Parasenecio*, and *Petasites*), and mining pattern without adjoining trajectories (the mine of the latter is characterized by adjoining meandering trajectories; Fig. 16B, E, I).

This new species also resembles *Clematis*-associated *Sphaeroderma* species (*C. unicolor* and yellow form of *C. uenoi*) in terms of habitus and body color. However, it is distinguished from the latter by the darker color of elytra compared to their yellowish color in *C. unicolor* and yellow color in *C. uenoi*, a pair of frontal tubercles contacting each other compared to distinct tubercles

in the latter (Takizawa 2021: figs 7, 10), and laterally almost uncurved aedeagus of the male genitalia compared to the significantly aedeagus in the latter (Takizawa 2021: figs 12, 15).

Fifteen species of *Sphaeroderma* have been recorded from Taiwan, 13 of which are endemic to the region (Kimoto and Takizawa 1997; Lee 2023). The newly identified species resembles *Sphaeroderma hsui* Lee, 2023, a Taiwanese species, in terms of its habitus and small size. However, it can be differentiated from the latter based on its dark brown antennae compared to the yellowish-brown antennae in the latter, transverse frontal tubercle compared to the rounded or subsquare frontal tubercle in the latter, laterally uncurved aedeagus of male genitalia compared to the laterally moderately curved aedeagus in the latter, and a slender spermathecal pump with an apical tubular appendage compared to a short pump without apical appendage in the latter.

Among 21 *Sphaeroderma* species recorded from Japan (Takizawa 2021), the following five species have no known host plants (Hayashi et al. 1984; Kimoto and Takizawa 1993):

Sphaeroderma atrum Jacoby, 1885
Sphaeroderma kuroashi Kimoto, 2000
Sphaeroderma morimotoi Chûjô & Ohno, 1964
Sphaeroderma obscurum Ohno, 1964
Sphaeroderma rubidum (Graells, 1858)

Cassidinae Gyllenhal, 1813
Hispini Gyllenhal, 1813
Leptispa Baly, 1858

Leptispa taguchii Chûjô, 1956

Host plant. Poaceae: *Miscanthus sinensis* Andersson (Hayashi et al. 1984; Kimoto and Takizawa 1993).

Leaf mine. Unknown.

Leptispa miyamotoi Kimoto, 1957

Host plant. Poaceae: *Miscanthus sinensis*, *Saccharum officinarum* L. (Hayashi et al. 1984; Kimoto and Takizawa 1993).

Leaf mine. Unknown.

Asamangulia Maulik, 1915

Asamangulia yonakuni (Kimoto & Gressitt, 1966)

Host plant. Poaceae: *Oryza sativa* L., *Miscanthus sinensis* (Hayashi et al. 1984; Kimoto and Takizawa 1993).

Leaf mine. Unknown.

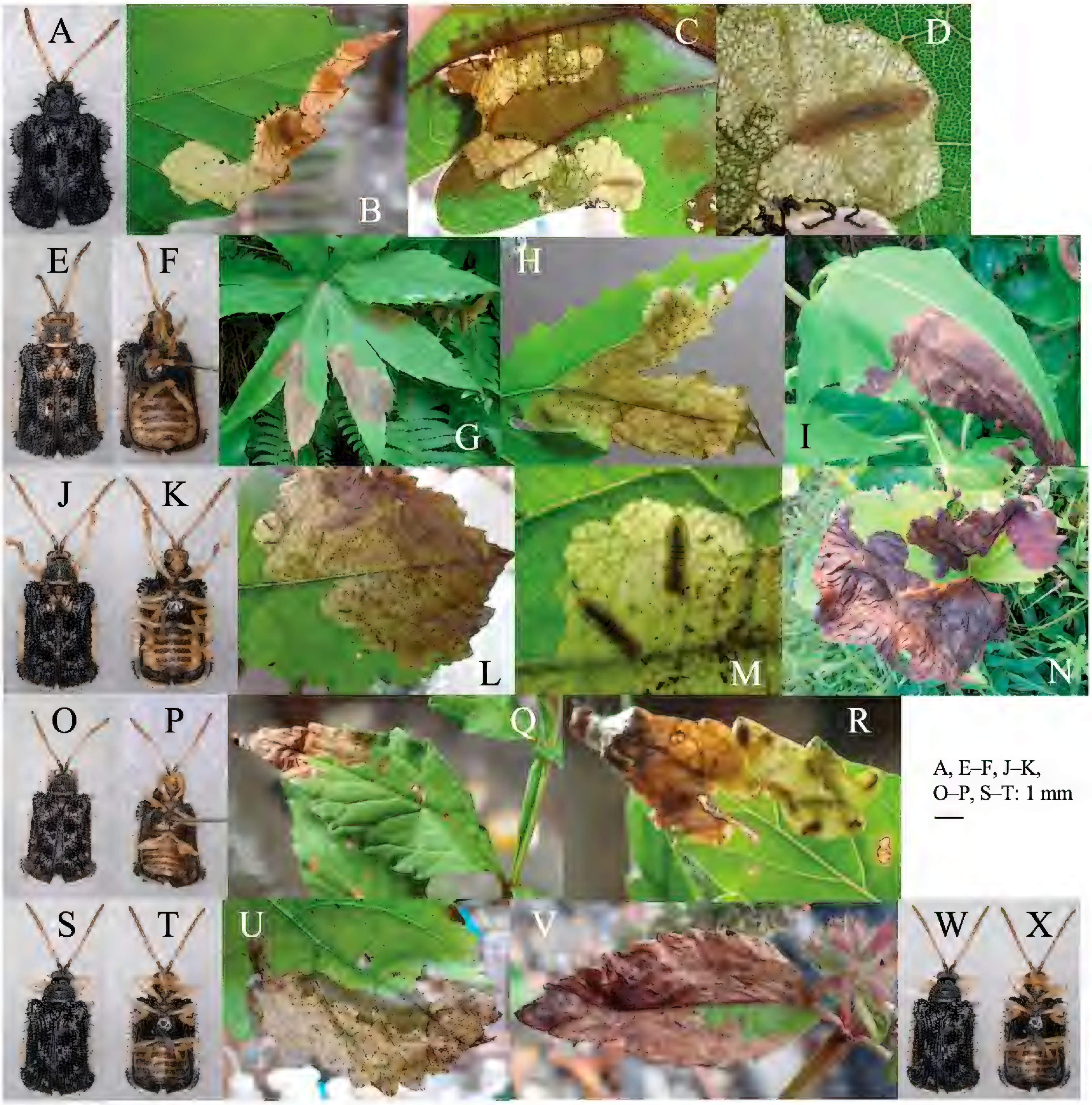

Figure 17. Habitus of adults and leaf mines of three *Dactylispa* species **A–D** *D. subquadrata* **E–N** *D. masonii* **O–X** *D. angulosa*. Host plants **A, B** *Quercus serrata* at Yashiro, Hyôgo Pref. **C, D** *Quercus dentata* at Nasu, Tochigi Pref. **E–H** *Syneilesis palmata* at Kawazu, Izu, Shizuoka Pref. **N–S** *Parasenecio hastatus* subsp. *orientalis* at Aikappu, Akkeshi, Hokkaido **J–M** *Cirsium suzukaense* at Mt. Ibuki, Shiga Pref. **N** *Ligularia hodgsonii* at Aikappu, Akkeshi, Hokkaido **O–R** *Salvia ranzaniana* at Sabushi-gawa, Niimi, Okayama Pref. **S–U** *Salvia nipponica* at Nasu, Tochigi Pref. **V** *Clinopodium micranthum* at Nagawado, Nagano Pref. **W–X** *Lithospermum zollingeri* at Taishaku-kyô, Okayama Pref.

Dactylispa Weise, 1897

Dactylispa subquadrata (Baly, 1874)
Fig. 17A–D

Host plant. Fagaceae: *Castanea crenata* Sieb. et Zucc., *Castanopsis sieboldii* (Makino), *Quercus dentata* Thunb., *Q. aliena* Blume, *Q. serrata* Thunb., *Q. variabilis* Blume, *Q. glauca* (Thunb.).

Leaf mine. Full-depth linear-blotch mine on mature leaf (Fig. 17B–D). The mine has many holes perforated by larva on each side of the mine, and frass is excreted outside through the holes. The fully grown larva pupates in the mine. The upper layer tissue around the pupation site is often kept intact, so that the pupa is hidden by the green tissue and kept less conspicuous.

Material examined. • 11 adults, Yashiro, Katô, Hyôgo Pref., 25-VI-2019 (as larva on *Quercus serrata*), emerged on 19–23-VII-2019 (Fig. 17A–C); Several leaf mines, Toyohara, Nasu, Tochigi Pref., 2-VII-2022 on *Quercus dentata* (Fig. 17D); • 1 adult, Hami, Miyazu, Kyoto Pref., 3-VIII-2008 (as larva on *Quercus variabilis*), emerged on 4-VIII-2008; • 1 adult, Hami, Miyazu, Kyoto Pref., 16-VII-2012 (as larva on *Q. glauca*), emerged on 1-VIII-2012; • 1 adult, Kushimoto-ôshima, Higashimuro-gun, Wakayama Pref., 2-VIII-1999 (as larva on *Castanopsis sieboldii*), emerged on 3-VIII-1999; • 1 adult, Hami, Miyazu, Kyoto Pref., 3-VIII-2008 (as larva on *Castanea crenata*), emerged on 5-VIII-2008.

Dactylispa masonii **Gestro, 1923**
Fig. 17E–N

Host plant. Asteraceae: *Ainsliaea acerifolia* Sch. Bip., *Aster yomena* (Kitam.), *Cacalia auriculata* DC. var. *kamtschatica* (Kitam.), *Cirsium ashiuense* S. Yokoy. et T. Shimizu, *C. confertissimum* Nakai, *C. inundatum* Makino, *C. kiotoense*, *C. longepedunculatum* Kitam., *C. microspicatum* Nakai, *C. okamotoi* Kitam., *C. olygophyllum* (Franch. et Sav.), *C. sieboldii* Miq., *C. suzukaense* Kitam., *C. tashiroi* Kitam. var. *hidaense* (Kitam.), *C. tonense* Nakai, *Ligularia fischeri* (Ledeb.), *L. hodgsonii* Hook., *Parasenecio hastatus* (L.) ssp. *orientalis* (Kitam.), *P. farfarifolius* (Siebold et Zucc.) var. *bulbiferus* (Maxim.), *Petasites japonicus*, *Syneilesis palmata* (Thunb.).

Leaf mine. Dark upper-layer aggregate blotch mine on mature leaf (Fig. 17G–I, L–N). Frass is granular, deposited along meandering larval trajectory. Often several larvae aggregately mine in a leaf, and the mined area is large and turns blackish. The fully grown larvae pupate together in the mine.

Material examined. • 20 adults, Kawazu, Kamo-gun, Shizuoka Pref., 7-VI-2015 (as larva on *Syneilesis palmata*), emerged on 15–20-VI-2015 (Fig. 17E–H); • 2 adults, Aikappu, Akkeshi, Hokkaidô, 4-VIII-2023 (as larva on *Parasenecio hastatus* ssp. *orientalis*), emerged on 19-VIII-2023 (Fig. 17I); • 4 adults, Hotokegaura, Sai-mura, Shimokita, Aomori Pref., 27-VII-2009 (as larva on *Parasenecio farfarifolius* var. *bulbiferus*), emerged on 24–28-VIII-2009; 1 adult, Renge-onsen, Itoigawa, Niigata Pref., 4-IX-1999 (as larva on *Ainsliaea acerifolia*), emerged on 15-IX-1999; • 2 adults, Suehiro, Akkeshi, Hokkaidô, 4-VIII-2023 (as larva on *Ligularia hodgsonii*), emerged on 19-VIII-2023 (Fig. 17N); • 5 adults, Hiruzen, Maniwa, Okayama Pref., 30-VII-2018 (as larva on *Ligularia fischeri*), emerged on 2–30-VII-2018; • 1 adult, Ashiu, Nantan, Kyoto Pref., 7-VIII-1991 (as larva on *Cirsium ashiuense*), emerged on 20-VIII-1991; 8 adults, Daigonji-kôgen, Matsunoyama, Tôkamachi, Niigata Pref., 19-VIII-2008 (as larva on *Cirsium inundatum*), emerged on 21–29-VIII-2008; • 5 adults, Aburazaka, Ôno, Fukui Pref., 6-IX-2019 (as larva on *Cirsium tashiroi* var. *hidaense*), emerged on 4–7-X-2019; • 5 adults, Koigakubo, Tessai, Niimi, Okayama Pref., 9-X-2017 (as larva on *Cirsium tashiroi* var. *hidaense*), emerged on 17-X-2017; • 5 adults, Niken-chaya, Shizuichi, Sakyô, Kyoto Pref., 10-VI-2015 (as larva

on *Cirsium kiotoense*), emerged on 30-VI-2015; 1 adult, Mt. Hakusan, Shiramine, Hakusan, Ishikawa Pref., 27-VII-1998 (as larva on *Cirsium matsumurae*), emerged on 20-VIII-1998; • 1 adult, Kaida-kôgen, Kiso, Nagano Pref., 7-VIII-2016 (as larva on *Cirsium oligophyllum*), emerged on 30-VIII-2016; • 1 adult, Toyohara, Nasu, Tochigi Pref., 30-VII-2018 (as larva on *Cirsium makinoi*), emerged on 3–20-VIII-2018; • 2 adults, Doai, Minakami, Tone-gun, Gunma Pref., 30-VII-2018 (as larva on *Cirsium microspicatum*), emerged on 3–20-VIII-2018; • 16 adults, Bibi, Chitose, Hokkaidô, 30-VI-2023 (as larva on *Petasites japonicus*), emerged on 24–26-VII-2023; 20 adults, Beppo, Nemuro, Hokkaidô, 23-VII-2018 (as larva on *Petasites japonicus*), emerged on 2–27-VIII-2018; • 6 adults, Kisofukushima, Kio Nagano Pref., 19-VII-1999 (as larva on *Petasites japonicus*), emerged on 2–11-VIII-1999;

Dactylispa angulosa **(Solsky, 1872)**

Fig. 17O–X

Host plant. Lamiaceae: *Clinopodium chinense* (Benth.) var. *parviflorum* (Kudo), *C. gracile* (Benth.), *C. micranthum* (Regel) var. *sachalinense* (F.Schmidt), *Isodon inflexa* Kudo, *Glechoma hederacea* (A.Gray), *Prunella vulgaris* L., *Salvia glabrescens* (Franch. et Sav.), *S. japonica* Thunb., *S. ranzaniana* Makino; Boraginaceae: *Lithospermum zollingeri* (A. DC.).

Leaf mine. Upper-layer aggregate blotch mine on mature leaf (Fig. 17Q, R, U, V). Frass is granular, deposited throughout the mine. The fully grown larva pupates in the mine.

Material examined. Lamiaceae: • 2 adults, Sabushi-gawa, Niimi, Okayama Pref., 20-VI-2020 (as larva on *Salvia ranzaniana*), emerged on 19–24-VII-2020 (Fig. 17O–R); • 4 adults, Toyohara, Nasu, Tochigi Pref., 2-VII-2022 (as larva on *Salvia glabrescens*), emerged on 19–25-VII-2022 (Fig. 17S–U); • 1 adult, Omotsubo, Tetta, Niimi, Okayama Pref., 19-VII-1991 (as larva on *Salvia japonica*), emerged on 21-VII-1991; • 3 adult, Kaida-kôgen, Kiso, Nagano Pref., 3-VIII-2002 (as larva on *Prunella vulgaris*), emerged on 21–28-VIII-2002; • 9 adults, Chigonosawa, Kisofukushima, Kiso, Nagano Pref., 20-VII-1997 (as larva on *Clinopodium chinense* var. *parviflorum*), emerged on 28-VII–1-VIII-1997; • 1 adult, Aburazaka, Ôno, Fukui Pref., 11-VII-2003 (as larva on *Clinopodium micranthum* var. *sachalinense*), emerged on 1-VIII-2003; • 1 adult, Nagawado, Matsumoto, Nagano Pref., 10-VIII-2016 (as larva on *Clinopodium micranthum*), emerged on 27-VIII-2016 (Fig. 17V); 1 adult, Chigonosawa, Kisofukushima, Kiso, Nagano Pref., 20-VII-1995 (as larva on *Isodon inflexus*), emerged on 5-VIII-2016; • 1 adult, Chigonosawa, Kisofukushima, Kiso, Nagano Pref., 20-VII-1995 (as larva on *Glechoma hederacea*), emerged on 10-VIII-1995; • 1 adult, Mumyôdani, Tetta, Niimi, Okayama Pref., 9-VII-1991 (as larva on *Meehania urticifolia*), emerged on ?-VIII-1991.

Boraginaceae: • 1 adult, Taishaku-kyô, Shôbara, Hiroshima Pref., 8-VII-1991 (as larva on *Lithospermum zollingeri*), emerged on ?-VIII-1991 (Fig. 17W–X).

Dactylispa higoniae **(Lewis, 1896)**

Fig. 18A–H

Host plant. Boraginaceae: *Callicarpa mollis* Siebold et Zucc.

Leaf mine. Upper-layer radiate mine on mature leaf, usually mining at the central part of the leaf (Fig. 18G, H). The mine has many holes perforated by larva along the margin of the mine, and frass is excreted outside through the holes. The fully grown larva pupates at central area just on midrib in the mine.

Material examined. Lamiaceae: • 2 adults, Inohae, Nichinan, Miyazaki Pref., 24-VII-2021 (as larva on *Callicarpa mollis*), emerged on 31-VII–1-VIII-2021 (Fig. 18A–H).

Dactylispa adinae **Kato, sp. nov.**
https://zoobank.org/299A7AE8-FE0C-4B87-8B81-133D498C38D1
Fig. 18I–W

Type locality. Japan: Miyazaki Pref., Nichinan, Inohae.

Type material. ***Holotype***: • ♂, Inohae, Nichinan, Miyazaki Pref. (31.728°N, 131.369°E, 85 m above sea level), 18-VII-2018 (as larva on *Adina pilulifera* collected by M. Kato), emerged on 1-VIII-2018 (NSMT-I-C-200360). ***Paratypes***: • 1 ♂ 2 ♀ same as holotype, emerged on 31-VII–6-VIII-2018 (NSMT-I-C-200361–200363); 1 ♀ Kaeda-keikoku, Miyazaki, Miyazaki Pref., 11-IV-2021 (as larva on *Adina pilulifera* by M. Kato), emerged on 26-V-2021 (NSMT-I-C-200365).

Additional material examined. • 1 ♂ 1 ♀ same as holotype, emerged on 3–14-VIII-2021; • 1 ♂ Kaeda-keikoku, Miyazaki, Miyazaki Pref., 11-IV-2021 (as larva on *Adina pilulifera*), emerged on 31-V-2021.

Diagnosis. This newly identified species exhibits a rectangular, flattened morphology (length: 4.6–4.7 mm), characterized by black, spiny pronotum and elytra, as well as a dull yellow ventral surface. The pronotum bears a pair of dull yellow trifurcate anterior spines and three pairs of dull yellow long spines oriented horizontally. Similarly, the elytron exhibits numerous long and short spines along margins and interstices I, II, IV, VI, and VIII. The male genitalia feature an aedeagus resembling a spatula in dorsal view, appearing almost parallel-sided and uncurved in lateral view. The larvae mine the leaves of Rubiaceae, particularly *Adina pilulifera*. This species resembles *Dactylispa nigrodiscalis* Gressitt, 1938, a Chinese species. However, it is differentiated from the latter by the widely separated anterior trifurcate spines of the prothorax and the basally separated first and second lateral spines on the prothorax.

Description. Male (Fig. 18I–Q). ***Habitus.*** The body is 4.6–4.7 mm in length (excluding spines) and is mostly black on the dorsal surface and dull yellow on the ventral surface and head (Fig. 18I, J). The pronotum is black except for dull yellow margins, spines, and a medial linear area before the posterior margin. The elytra are largely black except for dull yellow margins in the middle.

Head. The head is broader than the anterior margin of the prothorax, narrowing behind the eyes and with a black, smooth, and shining occiput. The frons is yellowish-brown and rugose, with a small projection between antennal insertions (Fig. 18M, arrow). The antennae are moderately long, approximately three-quarters of the body length. The segments do not feature spines and are covered with fine short hairs. Segment 1 is the longest among the 11 segments and is slightly curved outward. Segments 1 and 2 are dark brown, whereas segments 3–11 are yellowish brown. Segments 5–11 are slightly thicker than segments 3–4 (Fig. 18I). The proportional lengths of antennomeres 1–11 are as follows: 1:0.3:0.5:0.5:0.6:0.6:0.6:0.6:0.6:0.6:0.9.

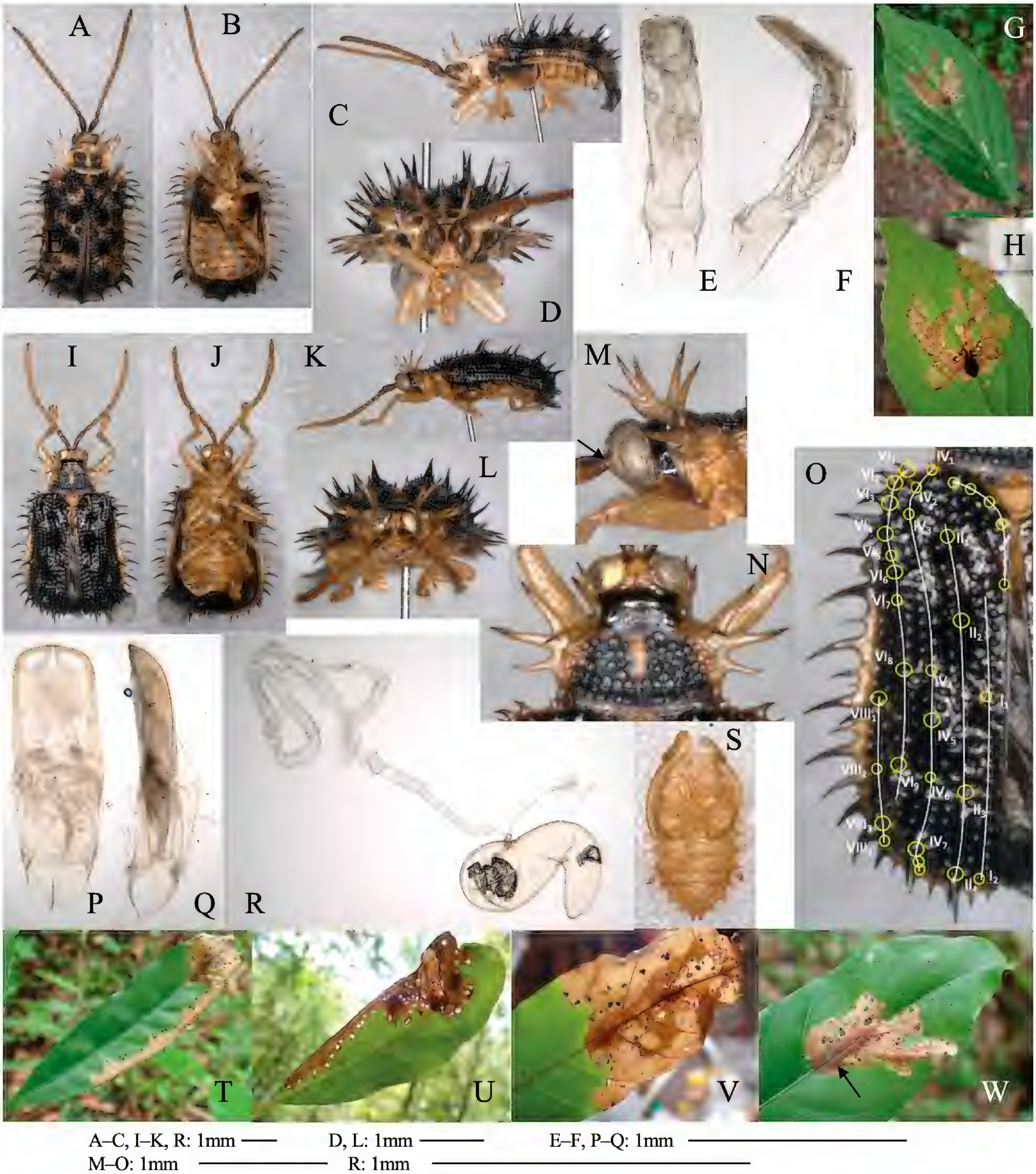

Figure 18. Adult morphology, male genitalia, and leaf mines of two *Dactylispa* species **A–H** *D. higoniae* **I–W** *D. adinae* sp. nov. **A–L** dorsal (**A, I**), ventral (**B, J**), lateral (**C, K**), frontal (**D, L**) views of adults **M** lateral view of prothorax **N** dorsal view of prothorax **O** arrangement of spines on interstices I–VIII of left elytra (yellow circles denote spines on interstices, size of circle indicates length of spine) **E, F, P–Q** aedeagus in male genitalia (**E, P** ventral, **F, Q** lateral) **R** spermatheca and ductus spermatheca in female genitalia **S** ventral view of pupal exuvia **G, H, T–W** leaf mines. Host plants **G, H** *Callicarpa mollis* **T–W** *Adina pilulifera* at Inohae, Nichinan, Miyazaki Pref. An arrow in **W** indicates pupation chamber.

***Thorax*.** The pronotum is transverse, measuring 1.6-fold as wide as long, with rounded sides that are prominently produced and flattened medially (Fig. 18I). A pair of dull yellow trifurcate spines appears at the anterior margin of the

pronotum (Fig. 18K, M). The two anterior projections share a long common stem and point upward, whereas the posterior projection points diagonally upward and backward, with black apexes. The lateral margin of the pronotum features three long, dull yellow spines pointed horizontally, with the anterior two being longer than the posterior one and located basally on a common stem. The apexes of the anterior two projections are black (Fig. 18N). The base of the disc features a transverse impression. The disc is granulated and covered with large punctures between the lateral spines, with a dull yellow, impunctate, longitudinal linear depression before the posterior margin along the median line.

The scutellum is finely granulose and broad but narrow and subangulate posteriorly. The elytra are largely parallel-sided and broadly rounded posteriorly, with distinct rounded punctures on the surface (Fig. 18I) that are largely black. However, the lateral margins in the middle and apical regions (including spines) are dull yellow. The base of the elytron is wider than the pronotum, with the sides and disc bearing numerous long spines. The lateral margin of the elytron is flattened on each side, featuring 15 or 16 compressed spines, with alternating long and short spines. Each long spine is as long as the first segment of the antenna and slightly curved backward. The apical margin is covered with seven or eight short spines. The elytral interstices are covered with long and short spines (Fig. 18K, O): interspace I with two short spines, interspace II with four long spines, interspace IV with nine spines of which the fifth and seventh are long, interspace VI with nine spines of which the fifth and seventh are short, and interspace VIII with four spines of which the first and third are long. Punctuation is regular and coarse, with the distance between punctures being smaller than the puncture diameter. The legs are dull yellow and slender.

***Abdomen*.** The abdomen is dull yellow.

***Genitalia*.** The aedeagus has a spatula-like appearance in dorsal view, with a poorly sclerotized basal region (Fig. 18P, Q). It measures 3-fold longer than its width, appearing almost parallel-sided and narrowed to a rounded apex. It is almost uncurved in lateral view. There are V-shaped phallobase apodeme rings around and keeling the median lobe.

Female. The body of females is larger than that of males, measuring 4.7–5.1 mm in length.

***Genitalia*.** The spermatheca is J-shaped and swollen (Fig. 18R). The cornu is gradually narrowed toward the blunt apex. The ductus spermatheca is thin, exceedingly elongated, and regularly and tightly coiled.

***Pupa*.** The body is pale brown, elongated, and flattened dorsoventrally (Fig. 18S). Abdominal segments I–IV feature acuminate bifurcated lateral processes at the apical region, with the ventral process smaller than the dorsal process. The processes of segment IV are significantly enlarged, and the ventral process is particularly thick and projecting diagonally backward, with a hooked tip. Segments V–VII feature bifurcated processes, with greater bifurcation of the ventral processes. Segments VIII and IX are fused, exhibiting two blunt processes apically.

Distribution. Around Obi, Southern Miyazaki Prefecture, Japan.

Host plants. Rubiaceae: *Adina pilulifera* (Lam.).

Leaf mine. Full-depth, linear-blotch mine on mature leaf, often transitioning into a radiate mine (Fig. 18T–W). The larvae create holes that penetrate the upper and lower layers of the leaf, with frass being discharged outside through

the holes. Holes form intermittent lines along the sides of the mine. Larvae sometimes exit the mine and move to another leaf to construct a new mine. Fully grown larvae pupate in the pupation chamber located nearly at the center of the mine, typically on the midrib. The upper layer of the leaf around the chamber remains undamaged and green.

Etymology. The species name refers to the genus name of the host plant, *Adina*.

Japanese name. Obi-togehamushi.

Remarks. *Dactylispa* exhibits considerable diversity in China (Chen et al. 1961; Chen and Tan 1964). This newly discovered species resembles *Dactylispa nigrodiscalis*, a Chinese species, in terms of its habitus, presence of trifurcate anterior spines on the prothorax, arrangement of spines on the elytra (Gressitt 1938), and association with the host plant family (Rubiaceae). However, it is differentiated from the latter by the presence of a pair of anterior trifurcate spines of the prothorax that are widely separated from each other, with the distance between spines being subequal to the width of the occiput but less than three-quarters of the width in the latter. The first and second lateral spines on the prothorax of the newly identified species branch basally, whereas in *D. nigrodiscalis*, the first and second lateral spines on the prothorax share common stems. Moreover, the former is associated with *Adina pilulifera* as the host plant species, whereas the latter is associated with *Metadina trichotoma*, *Mussaenda pubescens*, and *Uncaria rhynchophylla* (Yang et al. 2023). Given that *D. nigrodiscalis* belongs to the subgenus *Triplispa* (Zhang et al. 2021), this new species is considered a member of *Triplispa*.

This newly discovered species resembles *Dactylispa issikii* Chûjô, 1938 in terms of the presence of trifurcate anterior spines on the prothorax. However, it is distinguished from the latter by the presence of yellow spines on the prothorax compared to black in the latter, the presence of a yellow area on the pronotum and elytron compared to a black pronotum and elytron in the latter, completely yellow sternum compared to a dark brown sternum in the latter, more and shorter lateral spines on the elytron, and association with the host plant family Rubiaceae compared to Poaceae in the latter.

Although the new species is similar to *Dactylispa higoniae* in terms of habitus, it is distinguished from the latter by the presence of trifurcate anterior spines on the prothorax compared to bifurcate spines in the latter, yellow propleuron and sternum compared to their dark brown color in the latter except along the longitudinal suture, and association with the host plant family Rubiaceae compared to Lamiaceae for the latter.

Dactylispa issikii **Chûjô, 1938**

Fig. 19A–H

Host plant. Poaceae: *Pleioblastus chino* var. *viridis* (Makino), *P. simonii* (Carrière).

Leaf mine. White full-depth linear-blotch mine on mature leaf, usually situated around the leaf tip (Fig. 19F, G). Frass is granular, deposited linearly along either side of the mine, or discharged outside from a slit made along mine margin. The mine contains one or a few larvae, and the fully grown larva pupates in the mine.

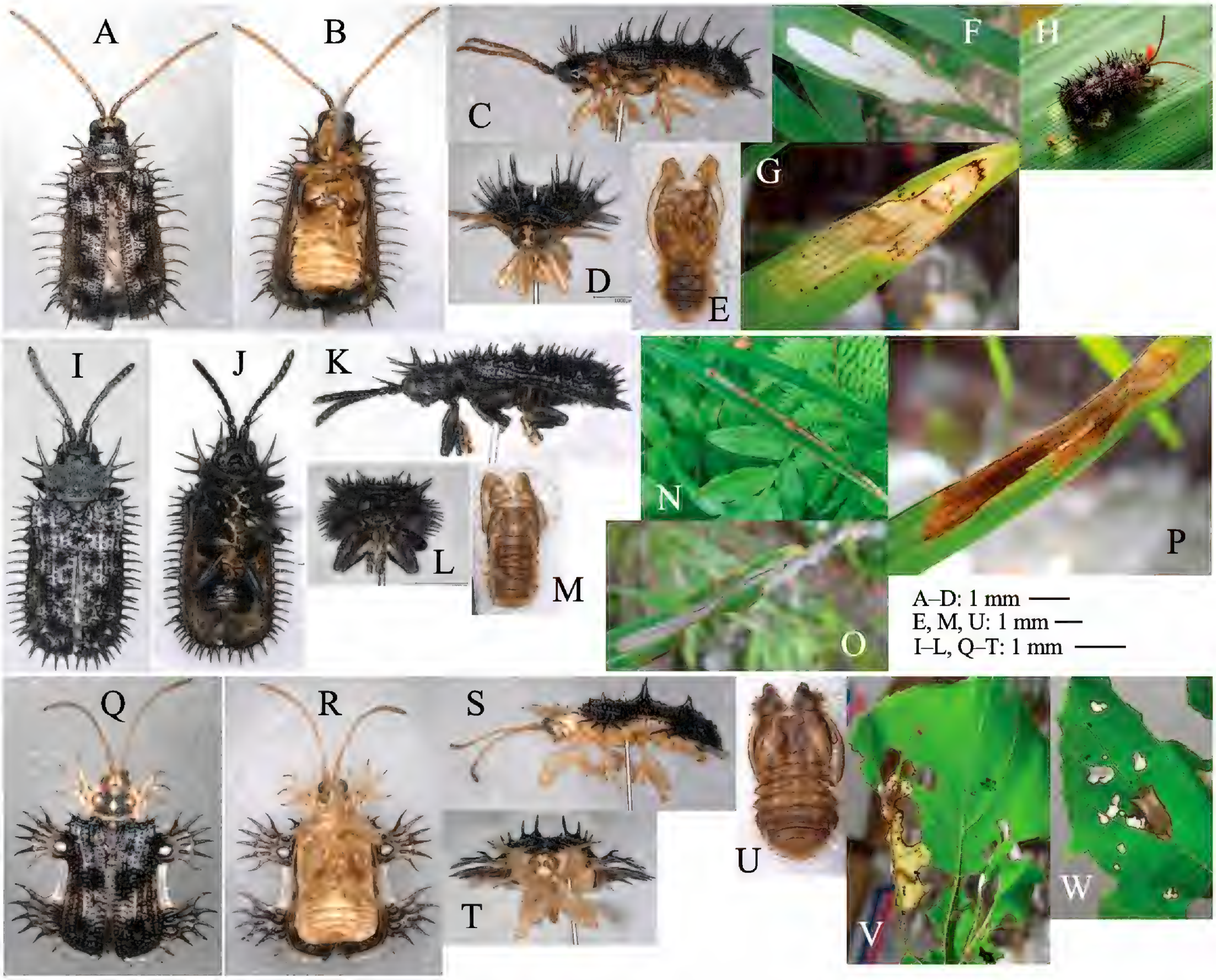

Figure 19. Adult morphology and leaf mines of three Hispini species **A–H** *Dactylispa issikii* **I–P** *Rhadinosa nigrocyanea* **Q–W** *Platypria melli* **A, I, Q** dorsal **B, J, R** ventral **C, K, S** lateral **D, L, T** frontal views of adults **E, M, U** exuviae **F, G, N–P, V, W** leaf mines. Host plants **G, H** *Pleioblastus chino* at Tsuge, Kuma, Kumamoto Pref. **B–O** *Miscanthus tinctorius* at Hatabe, Kumamoto Pref. **P** *Miscanthus tinctorius* at Fukube-dani, Hakusan, Ishikawa Pref. **V, W** *Hovenia dulcis* at Kin, Tsushima Is., Nagasaki Pref.

Material examined. • 8 adults, Tsuge, Ashikita, Ashikita-gun, Kumamoto Pref., 16-VII-2018 (as larva on *Pleioblastus chino* var. *viridis*), emerged on 20-VII–6-VIII-2018 (Fig. 19A–H); • 1 adult, Kyoto University, Yoshida, Sakyo, Kyoto Pref., 11-X-2015 (as larva on *P. chino* var. *viridis*), emerged on 15-XI-2015; • 6 adults, Fushimi-inari, Fushimi-ku, Kyoto Pref., 12-VII-2019 (as larva on *P. chino* var. *viridis*), emerged on 16–30-VII-2019; • 5 adults, Inohae, Nichinan, Miyazaki Pref., 14-VII-2021 (as larva on *P. simonii*), emerged on 19-VII–8-VIII-2021;

Hispellinus Weise, 1897

Hispellinus moerens (Baly, 1874)

Host plant. Poaceae: *Miscanthus sinensis* Anderss. (Hayashi et al. 1984; Kimoto and Takizawa 1993).

Leaf mine. Unknown.

***Rhadinosa* Weise, 1905**

***Rhadinosa nigrocyanea* (Motschulsky, 1860)**
Fig. 19I–P

Host plant. Poaceae: *Miscanthus condensatus* Hack., *M. sinensis*, *M. oligostachyus* Stapf, *M. tinctorius* (Steud.), *Pleioblastus chino* var. *viridis*.

Leaf mine. Upper-layer linear-blotch mine on mature leaf (Fig. 19N–P). Frass is granular, deposited along larval trajectory in the mine. The fully grown larva pupates in the mine.

Material examined. • 1 adult, Hatabe-gen'ya, Aso, Kumamoto Pref., 16-VII-2018 (as larva on *Miscanthus sinensis*), emerged on 21-VII-2018 (Fig. 19I–O); • 1 adult, Fukube-dani, Hakusan, Ishikawa Pref., 1-X-2019 (as larva on *M. tinctorius*), emerged on 14-X-2019 (Fig. 19P); • 2 adults, Mt. Kujû, Kokonoe, Kusu-gun, Ôita Pref., 27-IX-2019 (as larva on *M. oligostachyus*), emerged on 7–11-X-2019; • 1 adult, Mt. Yufu, Beppu, Ôita Pref., 23-VII-2017 (as larva on *Pleioblastus chino* var. *viridis*), emerged on 26-IX-2017.

***Platypria* Guérin-Méneville, 1840**

***Platypria melli* Uhmann, 1955**
Fig. 19Q–W

Host plant. Rhamnaceae: *Hovenia dulcis* Thunb.

Leaf mine. Full-depth blotch mine on the mature leaf (Fig. 19V). Frass is granular deposited in the mine. The larva sometimes relocates its mine. The fully grown larva pupates in the mine, sometimes in a mine newly constructed for pupation (Fig. 19W).

Material examined. • 1 adult, Kin, Kamitsushima Is., Tsushima, Nagasaki Pref., 3-VII-2015 (as larva on *Hovenia dulcis* collected by T. Kato), emerged on 9–16-VIII-2015 (Fig. 19Q–W).

***Dicladispa* Gestro, 1897**

***Dicladispa boutani* (Weise, 1905)**

Host plant. Poaceae: *Oryza sativa* (Kimoto and Takizawa 1987).

Leaf mine. Unknown.

Notosacanthini Gressitt, 1952
***Notosacantha* Chevrolat, 1837**

***Notosacantha ihai* Chûjô, 1958**
Fig. 20A–Y

Host plant. Proteaceae: *Helicia cochinchinensis* Lour.; Pentaphylacaceae: *Adinandra ryukyuensis* Masam., *Eurya japonica* Thunb.; Theaceae: *Schima liukiuensis* Nakai; Staphyleaceae: *Turpinia ternata* Nakai; Melastomataceae: *Bredia*

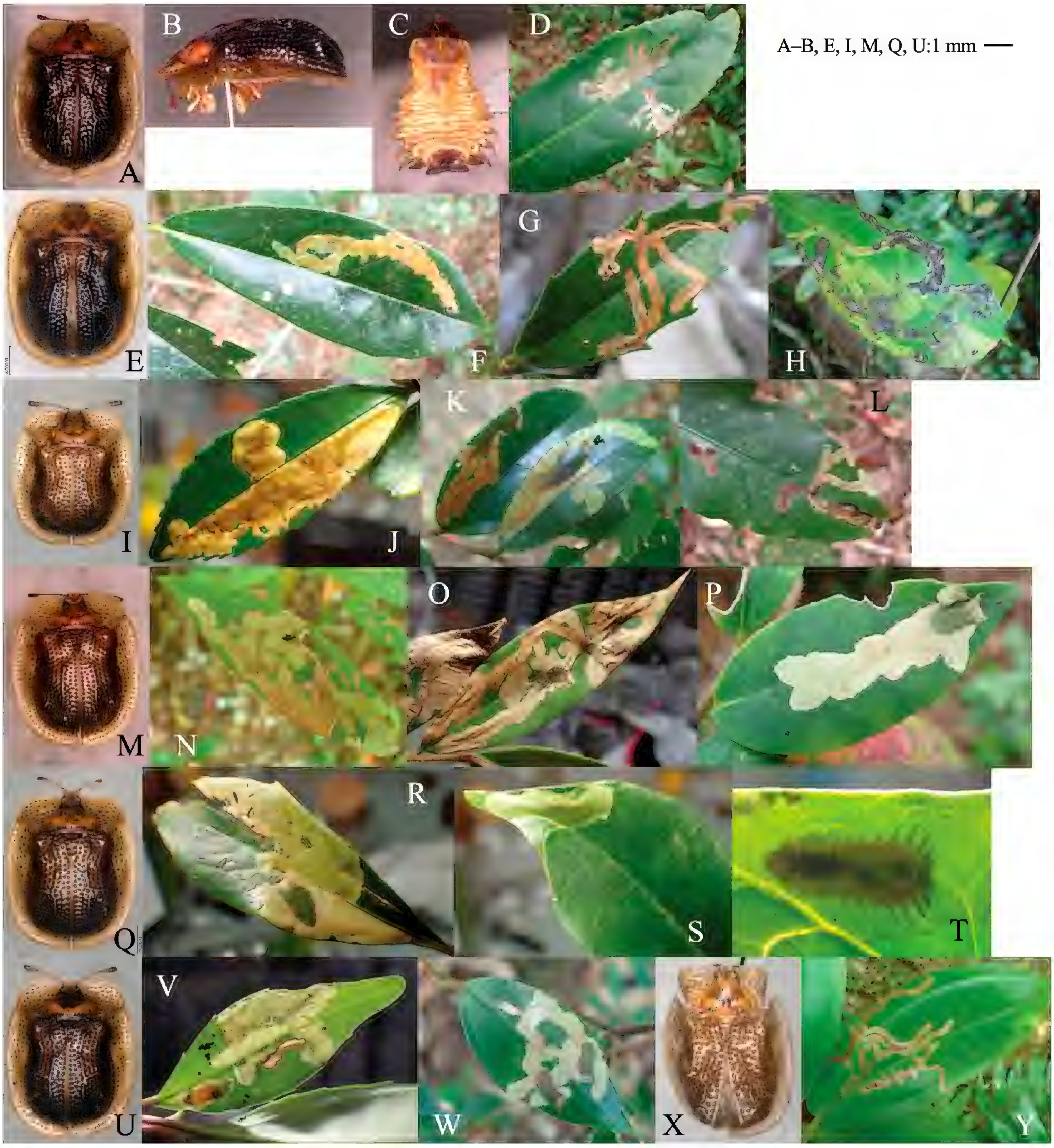

Figure 20. Adult habitus and leaf mines of *Notosacantha ihai* on various host plants **A–D** *Turpinia ternata* at Mt. Yuwan, Amami-ôshima, Kagoshima Pref. **E, F** *Symplocos glauca* at Yona, Kunigami, Okinawa Pref. **G** *Symplocos sonoharae* at Mt. Yuwan, Amami-ôshima, Kagoshima Pref. **H** *Gardneria nutans* at Mt. Nishime, Kunigami, Okinawa Pref. **I, J** *Eurya japonica* at Mt. Nishime, Kunigami, Okinawa Pref. **K** *Eurya japonica* at Yona, Kunigami, Okinawa Pref. **L** *Schima wallichii* at Mt. Yuwan, Amami-ôhsima, Kagoshima Pref. **M–P** *Adinandra ryukyuensis* at Yona, Kunigami, Okinawa Pref. **Q–T** *Helicia cochinchinensis* at Yona, Kunigami, Okinawa Pref. **U–W** *Bredia okinawensis* at Mt. Nishime, Kunigami, Okinawa **X, Y** *Bredia yaeyamensis* at Komi, Iriomote Is., Okinawa Pref.

okinawensis (Matsum.), *B. yaeyamensis* (Matsum.); Symplocaceae: *Symplocos glauca* (Thunb.), *S. sonoharae* Koidz.; Loganiaceae: *Gardneria liukiuensis* Hatus. All these plants are woody plants having coriaceous evergreen leaves.

Leaf mine. Upper-layer linear-blotch, often radiate mine on mature leaf (Fig. 20D, F–H, J–L, N–P, R–T, V–W, Y). The mine often has blind ends and branches, and the outline of the mine is often undulated. The larva sometimes relocates its mine. Frass

is granular, often discharged outside from slit made by the larva. The fully grown larva pupates in the mine, especially in the mine newly constructed for pupation.

Material examined. • 1 adult, Mt. Yuwan, Uken, Amami-ôshima Is., Kagoshima Pref., 25-V-2017 (as larva on *Turpinia ternata*), emerged on 15–18-VI-2017 (Fig. 20A–D); • 1 adult, Yona, Kunigami, Okinawa Is., Okinawa Pref., 19-V-2011 (as larva on *Symplocos glauca*), emerged on 13-VI-2011 (Fig. 20E, F); • 2 adults, Mt. Yuwan, Uken, Amami-ôshima Is., Kagoshima Pref., 29-IV-2005 (as larva on *Symplocos sonoharae*), emerged on 25-V-2005 (Fig. 20G); • 2 leaf mines, Mt. Nishime, Kunigami, Okinawa Pref., 17-III-2020 on *Gardneria liukiuensis* (Fig. 20H); • 1 adult, Mt. Nishime, Kunigami, Okinawa Is., Okinawa Pref., 17-III-2020 (as larva on *Eurya japonica* var. *japonica*), emerged on 9-V-2020 (Fig. 20I–K); • 2 leaf mines, Mt. Yuwan, Uken, Amami-ôshima Is., Kagoshima Pref., 23-XI-2023 on *Schima liukiuensis* (Fig. 20L); • 2 adults, Yona, Kunigami, Okinawa Is., Okinawa Pref., 29-III-2018 (as larva on *Adinandra ryukyuensis*), emerged on 4–9-V-2018 (Fig. 20M–P); • 3 adults, Yona, Kunigami, Okinawa Is., Okinawa Pref., 28-III-2018 (as larva on *Helicia cochinchinensis*), emerged on 30-IV–5-V-2018 (Fig. 20Q–T); • 1 adult, Mt. Nishime, Kunigami, Okinawa Is., Okinawa Pref., 17-III-2020 (as larva on *Bredia okinawensis*), emerged on 1-V-2020 (Fig. 20U–W); • 1 adult, Komi, Iriomote Is., Yaeyama, Okinawa Pref., 28-III-2018 (as larva on *Adinandra ryukyuensis*), emerged on 4-IV-2018 (Fig. 20X, Y).

Notosacantha loochooana **Chûjô, 1961**
Fig. 21A–F

Host plant. Iteaceae: *Itea oldhamii* Schneider; Rubiaceae: *Gardenia jasminoides* Ellis.

Leaf mine. The upper-layer linear-blotch, often radiate mine occurs on the mature leaf (Fig. 21D, F). The mine often has blind ends and branches. The larva sometimes relocates its mine. Frass is granular, often discharged outside from slit made by the larva. The fully grown larva pupates in the mine, often in a mine newly constructed for pupation.

Material examined. • 9 adults, Nagakumo-tôge, Amami-ôshima Is., Kagoshima Pref., 22-II-2015 (as larva on *Gardenia jasminoides*), emerged on 30-IV–1-V-2015 (Fig. 21A–D); 2 adults, Mt. Yui, Setouchi, Amami-ôshima Is., Kagoshima Pref., 19-III-1997 (as larva on *Gardenia jasminoides*), emerged on 1-V-1997; • 1 adult, Higashinakama, Sumiyo, Amami-ôshima, Kagoshima Pref., 21-II-2015 (as larva on *Itea oldhamii*), emerged on 4-V-2015 (Fig. 21E, F).

Notosacantha nishiyamai **Komiya, 2002**
Fig. 21G–O

Host plant. Rubiaceae: *Coptosapelta diffusa* (Champ. ex Benth.), *Gardenia jasminoides*, *Randia canthioides* Champ. ex Benth, *Tarenna gracilipes* Ohwi.

Leaf mine. Upper-layer linear-blotch, often radiate mine on mature leaf (Fig. 21J–K, N–O). The mine often has blind ends and branches. The larva sometimes relocates its mine. Frass is granular, often discharged outside from slit made by the larva. The fully grown larva pupates in a pupation site in the mine along the midrib, where upper layer of the leaf is kept intact and green (Fig. 21O).

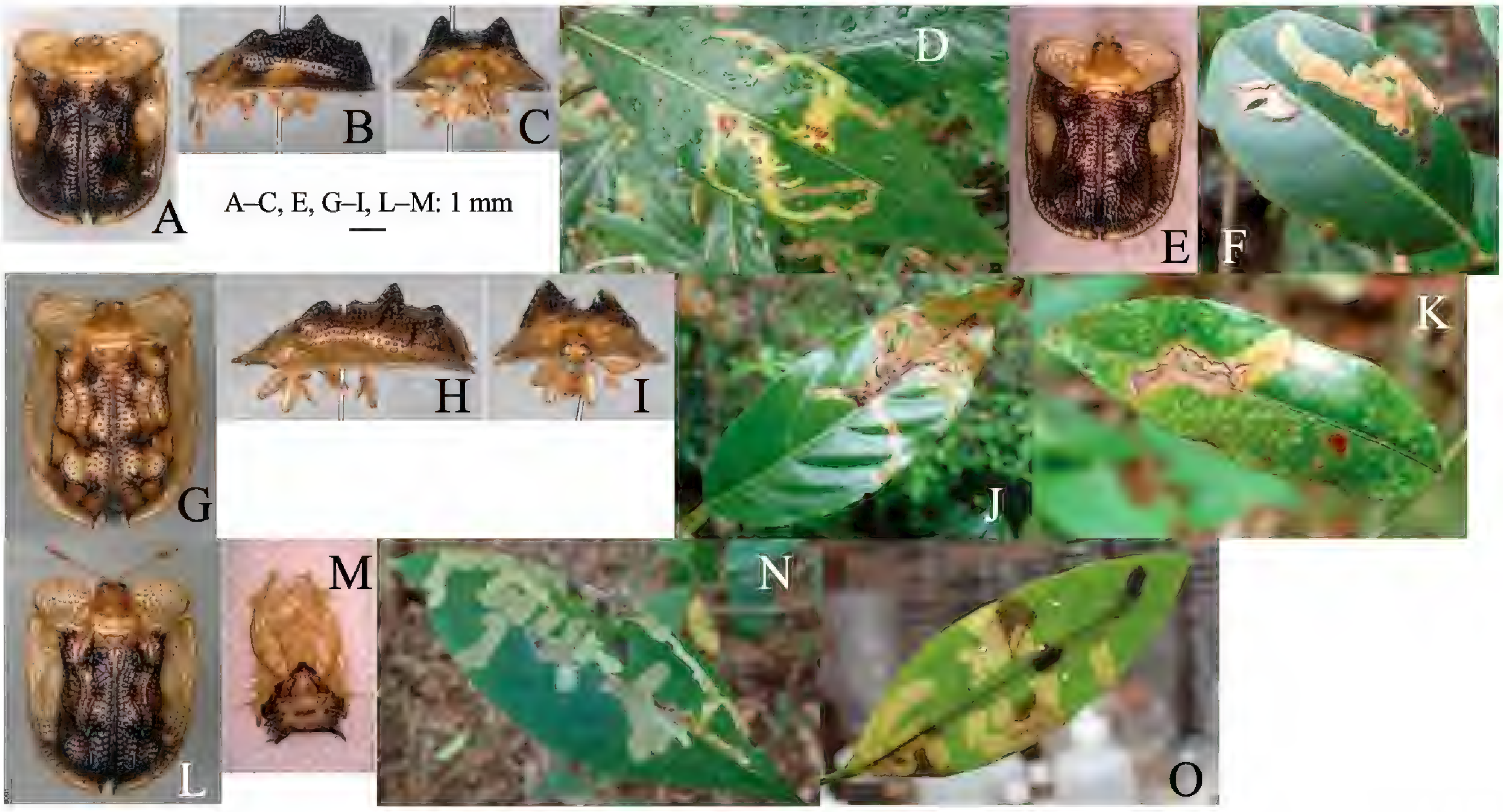

Figure 21. Habitus and leaf mines of two *Notosacantha* species **A–F** *Notosacantha loochooana* **G–O** *N. nishiyamai* **A, G, L** dorsal **B, H** lateral **C, I** frontal view of adults **M** exuvia **D, F, J, K, N, O** leaf mines. Host plants **A–D** *Gardenia jasminoides* at Nagakumo-toge, Amami-ôshima, Kagoshima Pref. **E, F** *Itea oldhamii* at Higashinakama, Amami-ôshima Is., Kagoshima Pref. **G–J** *Terenna gracilipes* at Nekumachiji, Ôgimi, Okinawa Pref. **K** *Coptosapelta diffusa* at Yona, Kunigami, Okinawa Pref. **L–O** *Randia canthioides* at Yona, Kunigami, Okinawa Pref.

Material examined. • 1 adult, Mt. Nekumachiji, Ôgimi, Okinawa Is. Okinawa Pref., 30-III-2018 (as larva on *Tarenna gracilipes*), emerged on 2-V-2018 (Fig. 21G–J); • 1 adult, Mt. Nishime, Kunigami, Okinawa Is., Okinawa Pref., 22-XII-1989 (as larva on *Gardenia jasminoides*), emerged on ?-IV-1990; • 2 leaf mines, Yona, Kunigami, Okinawa Is., Okinawa Pref., 29-III-2019 on *Coptosapelta diffusa* (Fig. 21K); • 2 adults, Yona, Kunigami, Okinawa Is., Okinawa Pref., 29-III-2018 (as larva on *Randia canthioides*), emerged on 3-V-2018 (Fig. 21L–O).

Discussion

Pattern of host plant utilization

Our study reviews the 64 leaf-mining beetle species of Chrysomeloidea within the Japanese Archipelago (Table 1), including the first description of leaf mines for 30 species. These species exhibit varied associations, including larvae found on pteridophytes (one species on Equisetales and four on Polypodiales), cycads (two species on Cycadales), and diverse angiosperms (66 species with 24 orders of angiosperms) (Table 2). Host plants are documented for the first time for six species: *Longitarsus holsaticus*, *Dibolia japonica*, *Psylliodes subrugosa*, *Halticorcus duodecimmaculata*, *Sphaeroderma komiana*, and *Dactylispa adinae* (Table 1). Host plant records are analyzed with the Chrysomelidae phylogeny of Nie et al. (2020), and suggest that host shifts from angiosperms to pteridophytes have likely occurred once or twice, in *Hippuriphila* and *Halticorcus* (Table 2). The mined part of *Equisetum* by *Hippuriphila* is a functional leaf but a botanical shoot. The larva of *Hippuriphila* do not exhibit the typical larval

body flattering characteristic observed in most leaf miners. Similar non-flattened leaf-mining larvae are found in the cerambycid larvae mining megasporophyll and leaf stalk of cycads.

All four *Halticorcus* species are associated with epiphytic or terrestrial evergreen ferns characterized by simple or unipinnate compound leaves, most of which are large, coriaceous, and sometimes fleshy. Each species uses multiple fern species, with *H. sauteri* utilizing specimens from six genera belonging to three families. While some *Halticorcus* species share host plant genera and species, sympatric species (e.g., *H. hiranoi* and *H. sauteri*) do not typically share the same host plant species, suggesting that host plant segregation likely played a role in speciation of *Halticorcus*.

Within the beetle clades associated with angiosperms, diversification has been noted in Polypodiales (*Halticorcus*), Rununculaceae (*Argopus* and *Sphaeroderma*), Celastraceae (*Zeugophora*), and Oleaceae in Lamiales (*Argopistes*) (Table 2). This suggests that diversification may have occurred through host shifts among different plant species and genera within the same genus or family. However, within each beetle genus, multiple species can share the same plant species. Rearing records suggest that diversification can also occur through the variations in the larval active seasons on the same host plants, without necessitating host shifts among plant species. For example, among the three *Zeugophora* species (*Z. annulata*, *Z. nigricolis*, and *Z. unifasciata*) associated with *Euonymus sieboldianus* (Fig. 2A–D, N–Q), *Z. annulata* exclusively mines newly opened leaves in early spring, *Z. nigricolis* targets fully opened leaves in June, and *Z. unifasciata* mines mature leaves between July and September.

Extended host specificity

Among the 64 species for which host plants were identified, 29 were specific to particular host species, 12 to host genera, 16 to host families, two to host orders, and five species were non-specific even to order level (Tables 1, 2). In species associated with multiple plant orders or families, each beetle species utilizes only a small number of plant genera or species, suggesting that they are far from generalists. This pattern of host selection can be referred to as extended host specificity, where species are restricted to host plant genera or species belonging to distinct plant orders and families.

Argopus punctipennis is a large red leaf-beetle commonly found on thistle. Our study revealed that this species is associated with 24 plant species distributed among three phylogenetically isolated genera (*Asarum*, *Aconitum*, and *Cirsium*) belonging to different families (Aristolochiaceae, Ranunculaceae, and Asteraceae) and orders (Piperales, Ranunculales, and Asterales) (Fig. 11A–S), illustrating extended host specificity. The combination of these three plant genera is intriguing, particularly because *Aconitum* contains diverse highly toxic metabolites (Ali et al. 2021) and is rarely infested by herbivores. Given that the other two *Argopus* species are associated with *Clematis* (Ranunculaceae), we hypothesize that an intra-familial host shift from *Clematis* to *Aconitum* occurred initially in *A. punctipennis*. Subsequently, inter-familial host shifts occurred, from *Aconitum* to *Asarum* and *Cirsium*. These beetles reared from various plant genera cannot be distinguished, even in terms of male genital morphology, suggesting that host races have not yet been differentiated.

Table 1. Leaf-mining species of Chrysomeloidea in Japan, with their host plants, host specificity, mining patterns and pupation sites.

Family	Subfamily	Tribe	Genus	Species	Host plants	No. utilized plant taxa				Mining pattern*	Ps**
						order	family	genur	species		
Cerambycidae	Lamiinae		*Mimectatina*	*meridiana ohirai*	**Cycadaceae**: *Cycas revoluta*	1	1	1	**1**	LBM	in
			Sybra	*ordinata*	**Cycadaceae**: *Cycas revoluta*	1	1	1	**1**	LBM	in
Megalopodinae	Zeugophorinae		*Zeugophora*	*annulata*	**Celastraceae**: *Celastrus orbiculatus, Euonymus alatus, E. sieboldianus, E. oxyphyllus, E. macropterus, E. tricarpus, E. melananthus, E. japonicus, E. fortunei, Tripterygium regelii*	1	**1**	3	10	LM	ex
				chujoi	**Celastraceae**: *Euonymus fortunei*	1	1	1	**1**	PM↓→LM	ex
				flavonotata	**Celastraceae**: *Euonymus tanakae, E. japonicus*	1	1	**1**	2	LM	ex
				nigricolis	**Celastraceae**: *Euonymus sieboldianus*	1	1	1	**1**	LBM	ex
				unifasciata	**Celastraceae**: *Euonymus sieboldianus*	1	1	1	**1**	LM	ex
				varipes	**Symplocaceae**: *Symplocos sawafutagi, S. coreana*	1	1	**1**	2	LBM	ex
				hozumii	**Salicaceae**: *Salix cardiophylla* var. *urbaniana*	1	1	1	**1**	LBM	ex
				japonica	**Salicaceae**: *Populus suaveolens*	1	1	1	**1**	LBM	ex
				cupka	**Salicaceae**: *Populus suaveolens*†	1	1	1	**1**	?	ex
				gracilis	?					?	?
Chrysomelidae	Alticinae	Alticini	*Phyllotreta*	*ezoensis*	**Brassicaceae**: *Draba nemorosa*	1	1	1	**1**	PM↔RM	ex
				shirahatai	**Brassicaceae**: *Cardamine leucantha*	1	1	1	**1**	LM	ex
			Longitarsus	*holsaticus*	**Plantaginaceae**: *Pennellianthus frutescens*	1	1	1	**1**	RM	ex
			Dibolia	*japonica*	**Lamiaceae**: *Stachys aspera* var. *hispidula*	1	1	1	**1**	LBM	ex
			Mantura	*clavareaui*	**Polygonaceae**: *Rumex japonicus, R. acetosa, Polygonum aviculare*	1	**1**	2	3	LBM	ex
				fulvipes	**Oxalidaceae**: *Oxalis corniculata*	1	1	1	**1**	LBM	ex
				japonica	?					?	?
			Hippuriphila	*babai*	**Equisetaceae**: *Equisetum arvense, E. fluviatile*	1	1	**1**	2	PM	ex
			Psylliodes	*punctifrons*	**Brassicaceae**: *Brassica juncea, Cardamine occulta, C. regeliana, Raphanus sativus* var. *raphanistroides, Rorippa palustris, Eutrema japonicum*	1	**1**	4	6	PM↔RM	ex
				subrugosa	**Brassicaceae**: *Arabis hirsuta*	1	1	1	**1**	PM↔RM	ex
			Halticorcus	*kasuga*	**Polypodiaceae**: *Lepisorus thunbergianus, L. onoei, L. miyoshianus*	1	1	**1**	3	LBM	ex
				sauteri	**Dryopteridaceae**: *Crytomium falcantum*; Oleandraceae: *Nephrolepis cordifolia*; **Polypodiaceae**: *Colysis elliptica, Loxogramme salicifolia, Leptochilus neopothifolius, Phymatosorus scolopendria*	**1**	3	6	6	LBM	ex
				hiranoi	**Aspleniaceae**: *Asplenium antiquum*; **Polypodiaceae**: *Pyrrosia lingua, Lemmaphyllum microphyllum, Lepisorus thunbergianus, Loxogramme salicifolia*; **Vittariaceae**: *Vittaria flexuosa*	**1**	3	6	6	LBM	ex
				duodecimmaculata	**Polypodiaceae**: *Phymatosorus scolopendria, Selliguea yakushimensis*	1	**1**	2	2	LBM	ex
			Argopistes	*coccinelliformis*	**Oleaceae**: *Ligustrum japonicum, L. micranthum, L. ovalifolium, Osmanthus heterophyllus*†*, O. zentaroanus, O.* × *fortunei*†	1	**1**	2	6	LBM	ex
				biplagiata	**Oleaceae**: *Ligustrum japonicum, Osmanthus heterophyllus, O. zentaroanus , O.* × *fortunei*	1	**1**	2	3	LBM	ex
				unicolor	**Oleaceae**: *Osmanthus heterophyllus*†	1	1	1	**1**	LBM	ex
				ryukyuensis	**Oleaceae**: *Ligustrum japonicum*	1	1	1	**1**	LBM	ex

Family	Subfamily	Tribe	Genus	Species	Host plants	No. utilized plant taxa				Mining pattern*	Ps**
						order	family	genur	species		
				tsekooni	**Oleaceae**: *Ligustrum obtusifolium*, *Fraxinus sieboldiana*, *Syringa reticulata*	1	**1**	3	3	LBM	ex
			Argopus	*balyi*	**Ranunculaceae**: *Clematis stans*, *C. apiifolia*†, *Clematis terniflora*†	1	1	**1**	2	LBM	ex
				clypeatus	**Ranunculaceae**: *Clematis terniflora*, *C. apiifolia*†	1	1	**1**	2	LBM	ex
				punctipennis	**Aristolochiaceae**: *Asarum heterotropoides*, *A. tohokuense*, *A. sieboldii*, *A. caulescens*, *A. megacalyx*, *A. blumei*, *A. curvistigma*, *A. asperum*, *A. nipponicum*; **Ranunculaceae**: *Aconitum pterocaule*, *A. gigas*, *A. sachalinense*, *A. japonicum*, *A. okuyamae*; **Asteraceae**: *Cirsium japonicum*, *C. kiotoense*, *C. yoshinoi*, *C. taishakuense*, *C. otayae*, *C. microspicatum*, *C. ugoense*, *C. otayae*, *C. makinoi*, *C. kamtschaticum*, *C. austrohidakaense*	**1**	3	3	25	LBM	ex
				clarki	?					?	?
				nigripennis	?					?	?
				unicolor	?					?	?
			Sphaeroderma	*nigricolle*	**Liliaceae**: *Cardiocrinum cordatum*, *Lilium auratum*, *Tricyrtis macropoda*, *T. flave*, Smilacaceae: *Smilax china*, *Smilax riparia*, *S. nipponica*, *S. stans*, *Heterosmilax japonica*; **Stemonaceae**: *Croomia heterosepala*, *C. japonica*	**1**	3	6	11	LBM	ex
				japanum	**Commelinaceae**: *Commelina communis*	1	1	1	**1**	LBM	ex
				tarsatum	**Poaceae**: *Phyllostachys bambusoides*, *P. bambusoides*, *Pleioblastus chino* var. *viridis*, *Sasa kurilensis*, *S. senanensis*, *S. nipponica*, *Sasamorpha borealis*, *Shibataea kumasaca*, *Stipa coreana* var. *kengii*	1	**1**	6	9	LBM	ex
				seriatum	**Poaceae**: *Panicum bisulcatum*	1	1	1	**1**	LBM	ex
				apicale	**Poaceae**: *Miscanthus sinensis*†	1	1	1	**1**	LBM	ex
				fulvoapicale	?					?	?
				akebia	**Lardizabalaceae**: *Akebia trifoliata*, *A. quinata*	1	1	**1**	2	BM	ex
				inaizumii	**Lardizabalaceae**: *Akebia trifoliata*, *A. quinata*	1	1	**1**	2	BM	ex
				quadrimaculatum	**Ranunculaceae**: *Clematis taiwaniana* var. *ryukiuensis*	1	1	1	**1**	LBM	ex
				flavonotatum	**Ranunculaceae**: *Clematis pierotii*	1	1	1	**1**	LBM	ex
				placidum	**Ranunculaceae**: *Clematis apiifolia*	1	1	1	**1**	BM	ex
				unicolor	**Ranunculaceae**: *Clematis terniflora*, *C. apiifolia*	1	1	**1**	2	LM	ex
				uenoi	**Ranunculaceae**: *Clematis apiifolia*, *C. terniflora*	1	1	**1**	2	LBM	ex
				ohkuboi	**Ranunculaceae**: *Cimicifuga japonica*, *C. biternata*, *C. simplex*	1	1	**1**	3	LBM	ex
				separatum	**Ranunculaceae**: *Clematis apiifolia*†	1	1	1	**1**	LBM	ex
				balyi	**Asteraceae**: *Farfugium japonicum*, *Parasenecio kamtschaticus*, *P. amagiensis*, *P. yatabei*, *Petasites japonicus*	1	**1**	3	5	LBM	ex
				komiana sp. nov.	**Asteraceae**: *Ixeris japonica*, *Lactuca indica*, *Youngia japonica*	1	**1**	3	3	LBM	ex
				atrum	?					?	?
				morimotoi	?					?	?
				nigripes	?					?	?
				obscurum	?					?	?
				rubidum	?					?	?
	Cassidinae	Hispini	*Leptispa*	*taguchii*	**Poaceae**: *Miscanthus sinensis*†	1	1	1	**1**	LM	in

Family	Subfamily	Tribe	Genus	Species	Host plants	No. utilized plant taxa				Mining pattern*	Ps**
						order	family	genur	species		
				miyamotoi	**Poaceae**: *Miscanthus sinensis*†, *Saccharum officinarum*†	1	**1**	2	2	LM	in
			Asamangulia	*yonakuni*	**Poaceae**: *Oryza sativa*†, *Miscanthus sinensis*†	1	**1**	2	2	LBM	in
			Dactylispa	*subquadrata*	**Fagaceae**: *Castanea crenata*, *Castanopsis sieboldii*, *Quercus dentata*, *Q. aliena*, *Q. serrata*, *Q. variabilis*, *Q. glauca*	1	**1**	3	7	LBM	in
				masonii	**Asteraceae**: *Ainsliaea acerifolia*, *Aster yomena*, *Cacalia auriculata* var. *kamtschatica*, *Cirsium microspicatum* var. *kiotoense*, *C. ashiuense*, *C. longepedunculatum*, *C. inundatum*, *C. tonense*, *C. olygophyllum*, *C. microspicatum*, *C. okamotoi*, *C. confertissimum*, *C. suzukaense*, *C. sieboldii*, *C. tashiroi* var. *hidaense*, *Ligularia fischeri*, *L. hodgsonii*, *Parasenecio hastatus* ssp. *orientalis*, *P. farfarifolius* var. *bulbiferus*, *Petasites japonicus*, *Syneilesis palmata*	1	**1**	8	21	LBM	in
				angulosa	**Lamiaceae**: *Clinopodium chinense* subsp. *grandiflorum*, *C. micranthum* var. *sachalinense*, *C. gracile*, *Isodon inflexa*, *Glechoma hederacea*, *Prunella vulgaris*, *Salvia japonica*, *S. ranzaniana*, *S. glabrescens*; **Boraginaceae**: *Lithospermum zollingeri*	**1**	2	5	10	LBM	in
				higoniae	**Boraginaceae**: *Callicarpa mollis*	1	1	1	**1**	LBM	in
				adinae sp. nov.	**Rubiaceae**: *Adina pilulifera*	1	1	1	**1**	LBM	in
				issikii	**Poaceae**: *Pleioblastus chino* var. *viridis*, *P. simonii*	1	1	**1**	2	LBM	in
			Hispellinus	*moerens*	**Poaceae**: *Miscanthus sinensis*†	1	1	1	**1**	LBM	in
			Rhadinosa	*nigrocyanea*	**Poaceae**: *Miscanthus sinensis*, *M. condensatus*, *M. tinctorius*, *M. oligostachyus*, *Pleioblastus chino* var. *viridis*	1	**1**	2	5	LBM	in
			Platypria	*melli*	**Rhamnaceae**: *Hovenia dulcis*	1	1	1	**1**	BM	in
			Dicladispa	*boutani*	**Poaceae**: *Oryza sativa*†	1	1	1	**1**	LBM	in
		Notosacanthini									
			Notosacantha	*ihai*	**Proteaceae**: *Helicia cochinchinensis*; **Pentaphylacaceae**: *Adinandra ryukyuensis*, *Eurya japonica* var. *japonica*; **Theaceae**: *Schima liukiuensis*; Staphyleaceae: *Turpinia ternata*; Melastomataceae: *Bredia okinawensis*, *B. yaeyamensis*; **Symplocaceae**: *Symplocos glauca*, *S. sonoharae*; **Loganiaceae**: *Gardneria liukiuensis*	4	7	8	10	RM	in
				loochooana	**Iteaceae**: *Itea oldhamii*; **Rubiaceae**: *Gardenia jasminoides*	2	2	2	2	RM	in
				nishiyamai	**Rubiaceae**: *Coptosapelta diffusa*, *Gardenia jasminoides*, *Randia canthioides*, *Tarenna gracilipes*	1	**1**	4	4	RM	in

† host plant species reported by refecences. * LM, linear mine; BM, blotch mine; LBM, linear–blotch mine; RM, radiate mine; PM, petiole/midrib mine; ↓, leaf fall. ** Pupation site: in, internal; ex, external.

The distribution of *Argopus punctipennis* (Fig. 22) suggests that the two or three plant genera are sympatric and simultaneously utilized at several sites, with no geographical patterns of host utilization. To explain why these three phylogenetically isolated genera are utilized by beetles, chemical analysis of secondary metabolites among host plant genera, bioassays of the beetles against these chemicals, genetic analysis of beetle populations, and phylogenetic analyses of individuals associated with different plant species or genera would be necessary.

Table 2. Host plant orders associated with Japanese leaf-mining species of Chrysomeloidea. Plant orders are arranged according to the system described by Ruggiero et al. (2015).

Beetle family	Genus	Species	Plant order																										
			Equisetales	Polypodiales	Cycadales	Piperales	Dioscorales	Pandanales	Liliales	Poales	Commelinales	Ranunculales	Proteales	Saxifragales	Celastrales	Oxalidales	Malpighiales	Rosales	Fagales	Myrtales	Crossosomatales	Brassicales	Caryophyllales	Ericales	Gentianales	Boraginales	Lamiales	Asterales	Total no. orders
Cerambycidae	*Mimectatina*	*meridiana ohirai*			1																								1
	Sybra	*ordinata*			1																								1
Megalopodinae	*Zeugophora*	*annulata*													1														1
		chujoi													1														1
		flavonotata													1														1
		nigricolis													1														1
		unifasciata													1														1
		varipes																						1					1
		hozumii															1												1
		japonica															1												1
		cupka															1												1
Chrysomelidae	*Phyllotreta*	*ezoensis*																				1							1
		shirahatai																				1							1
	Longitarsus	*holsaticus*																				1							1
	Dibolia	*japonica*																									1		1
	Mantura	*clavareaui*																					1						1
		fulvipes														1													1
	Hippuriphila	*babai*	1																										1
	Psylliodes	*chujoe*																				1							1
		punctifrons																				1							1
	Halticorcus	*kasuga*		1																									1
		sauteri		1																									1
		hiranoi		1																									1
		duodecimmaculata		1																									1
	Argopistes	*coccinelliformis*																									1		1
		biplagiata																									1		1
		unicolor																									1		1
		ryukyuensis																									1		1
		tsekooni																									1		1
	Argopus	*balyi*										1																	1
		clypeatus										1																	1
		*punctipennis**				1						1																1	3
	Sphaeroderma	*nigricolle**					1	1	1																				3
		japanum									1																		1
		tarsatum								1																			1
		seriatum								1																			1
		apicale								1																			1
		akebia										1																	1
		inaizumii										1																	1
		placidum										1																	1
		unicolor										1																	1
		uenoi										1																	1
		separatum										1																	1
		quadrimaculatum										1																	1

Beetle family	Genus	Species	Plant order																									
			Equisetales	Polypodiales	Cycadales	Piperales	Dioscorales	Pandanales	Liliales	Poales	Commelinales	Ranumculales	Proteales	Saxifragales	Celastrales	Oxalidales	Malpighiales	Rosales	Fagales	Myrtales	Crossosomatales	Brassicales	Caryophyllales	Ericales	Gentianales	Boraginales	Lamiales	Asterales	Total no. orders
		flavonotatum										1																	1
		ohkuboi										1																	1
		balyi																										1	1
		komiana sp. nov.																										1	1
	Liptispa	*taguchii*								1																			1
		miyamotoi								1																			1
	Asamangulia	*yonakuni*								1																			1
	Dactylispa	*subquadrata*																	1										1
		masonii																										1	1
		*angulosa**																								1	1		2
		higoniae																								1			1
		adinae sp. nov.																							1				1
		issikii								1																			1
	Hispellinus	*moerens*								1																			1
	Rhadinosa	*nigrocyanea*								1																			1
	Platypria	*melli*																1											1
	Dicladispa	*boutani*								1																			1
	Notosacantha	*ihai**											1							1	1			1					4
		*loochooana**												1											1				2
		*nishiyamai**																							1				1
Total number of beetle species				4	2	1	1	1	1	10	1	12	1	1	5	1	3	1	1	1	1	5	1	2	3	2	7	4	72

* The beetle species exibiting extended host specificity.

In Japan, the host plant genus *Asarum* (Aristolochiaceae) comprises locally restricted diverse species belonging to three sections: deciduous *Asarum* and *Asiasarum* and evergreen *Heterotropa* (Okuyama et al. 2020). Species from the *Asiasarum* section and several species from *Heterotropa* are utilized by two butterfly species, *Luerhdorfia puziloi* Leech, 1889 and *Luerhdorfia japonica* Leech, 1889 (Papilionidae), which utilize *Asiasarum* and *Heterotropa*, respectively. A recent molecular study revealed that the differential adaptation to various *Asarum* sections between the two *Luehdorfia* species and the reproductive interference between these species have influenced the formation of their current parapatric distribution (Suzuki et al. 2023). In contrast to *Luehdorfia*, *A. punctipennis* utilizes all three groups of *Asarum*, i.e., section *Asiasarum* in the *L. puziloi* range and sections *Heterotropa* and *Asarum* in the *L. japonica* range (Fig. 22). The difference in geographical host utilization patterns between *Luerhdorfia* and *A. punctipennis* may be attributable to variation in the time spent associating with *Asarum*. The association between *Luerhdorfia* and *Asarum* species is ancient, with divergence occurring approximately 17 million years ago (Suzuki et al. 2023). Conversely, the association between *A. punctipennis* and *Asarum* is of more recent origin, involving a host switch to *Asarum*.

The host genus *Cirsium* (Asteraceae) has undergone significant radiation in the Japanese archipelago (Ohashi et al. 2015), with most of the 150 recorded species being newly endemic. Diverse *Cirsium* species are utilized by *A. punctipennis* from Hokkaidô to Honshû. Additionally, *Cirsium* is utilized by two endemic

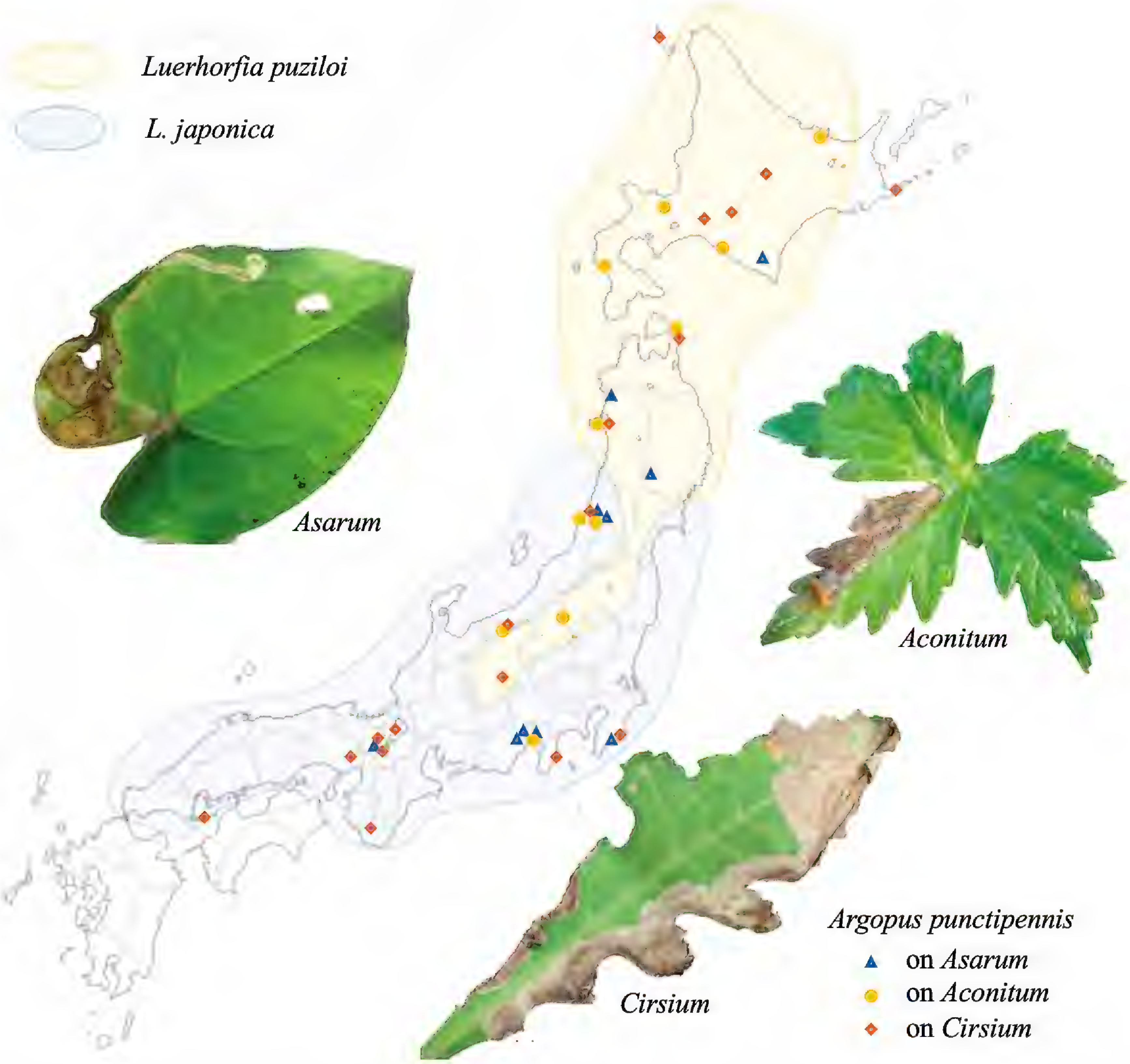

Figure 22. Map showing collection sites of *Argopus punctipennis* in the Japanese Archipelago with each recorded host plant genus (*Asarum*, *Aconitum* and *Cirsium*) indicated by different symbols. The distributions of two *Asarum*-associated butterfly species, *Luerhdorfia puziloi* and *L. japonica*, are presented (Suzuki et al. 2023).

phytophagous coccinellid beetle species, *Epilachna pustulosa* Kôno, 1937 and *Epilachna niponica* Lewis, 1896, in Hokkaidô and Honshû, respectively (Katakura, 1997). Recent phylogenetic analyses have revealed that the *Cirsium*-associated *Epilachna* species derived from a Solanaceae-associated clade, which diverged from Cucurbitaceae-associated Asian clades (Katoh et al. 2014). These results suggest that the routes and timing of host shifts to *Cirsium* differ between *Argopus* and *Epilachna*; the host shift in the former occurred more recently from Ranunculaceae, without differentiation between populations on different host plants. Conversely, in the case of *Epilachna*, the host shift from Solanaceae occurred earlier, resulting in the differentiation of *Cirsium*-associated species and subsequent differentiation of the two allopatric species.

Leaf-mining beetle species often utilize distinct host plant species at different sites within their range of distribution. *Sphaeroderma balyi* utilizes three genera of the tribe Senecioneae within the Asteraceae family, most of which are perennials with large, round leaves (Fig. 16A–J) that are widely distributed

in various climatic zones. These host plant genera vary among climatic zones. In cool temperate forests, the beetle species utilize deciduous perennials belonging to *Parasenecio* and *Petasites*, whereas in warm temperate forests, they utilize evergreen perennials belonging to *Farfugium*, with no overlap in their ranges (Fig. 23). Although the leaves of these host plant genera differ in terms of deciduousness, thickness, toughness, shape, and surface coating, their mining patterns are similar, suggesting that the expansion of the host range of *S. balyi* has occurred recently and is ongoing.

In Cassidinae, leaf-mining habit has evolved in two tribes Notosacanthini and Hispini, which respectively comprises 254 and 611 species in the world (Chaboo 2007). In Notosacanthini, extended host specificity was observed for all Japanese species of *Notosacantha* (Cassidinae: Notosacanthini), which construct radiate mines on coriaceous leaves of evergreen woody plants (Figs 20, 21). For example, *N. ihai* utilizes seven restricted genera belonging to seven phylogenetically isolated plant families as host plants. Similar pattern of host association is reported in several tropical *Notosacantha* species (Monteith et al. 2021). Cassidine leaf beetles, including *Notosacantha*, harbor host-specific gammaproteobacterial symbionts in gut-associated symbiotic organs, which help the host to digest food plants by producing pectin-degrading enzymes (Fukumori et al. 2022). In contrast with Notosacanthini, beetles in Hispini do not harbor gammaproteobacterial symbionts and show higher host specificity, suggesting that gammaproteobacterial symbionts may contribute to the extended host specificity of *Notosacantha*.

Mining patterns

Characteristic mining patterns described by Frost (1924) as being common to chrysomeloidean leaf miners was not found universally. Instead, their leaf mines are linear, linear-blotch, blotch, or radiate mines (Table 1). Larvae of Megalopodidae and Galerucinae are slightly flattened but still thick, and typically construct full-depth leaf mines, whereas larvae of Cassidinae are sufficiently flattened to construct upper-layer leaf mines. The pupation site is internal in Cerambycidae and Cassidinae but external (i.e., underground) in Megalopodidae and Galerucinae. Frass is typically left behind within its mine in a granular, linear, or meandering linear fashion in most groups except for several species of Hispini in Cassidinae, where frass is discharged outside through perforated holes. Abandoning and reconstructing mines (i.e., mine moving) are observed in various genera in Chrysomelidae, particularly on small leaves and those that wilt easily.

Unique midrib mining behavior was observed in *Zeugophora chujoi*, whose young instar larvae enter the midrib and cause the fall of newly opened leaves of *E. fortunei* (Fig. 2G–I). Similar midrib/petiole mining behaviors in young instars have been observed in a few buprestid species associated with Symplocaceae (Kato and Kawakita 2023). Another petiole/midrib miner is *Psylliodes punctifrons*, whose larvae mine the petiole/midrib of mature leaves of crucifer but do not cause leaf fall or wilting (Fig. 7C–E, H–J, L–P). The larva is not flattened but elongated, and its mine is not sufficiently thick to cause profound leaf damage. This slender larval morphology suggests that the leaf-mining habit has recently evolved from stem or root-mining habits, as *Psylliodes* species associated with the Brassicaceae are internal feeders in stems or roots (Gikonyo et al. 2019).

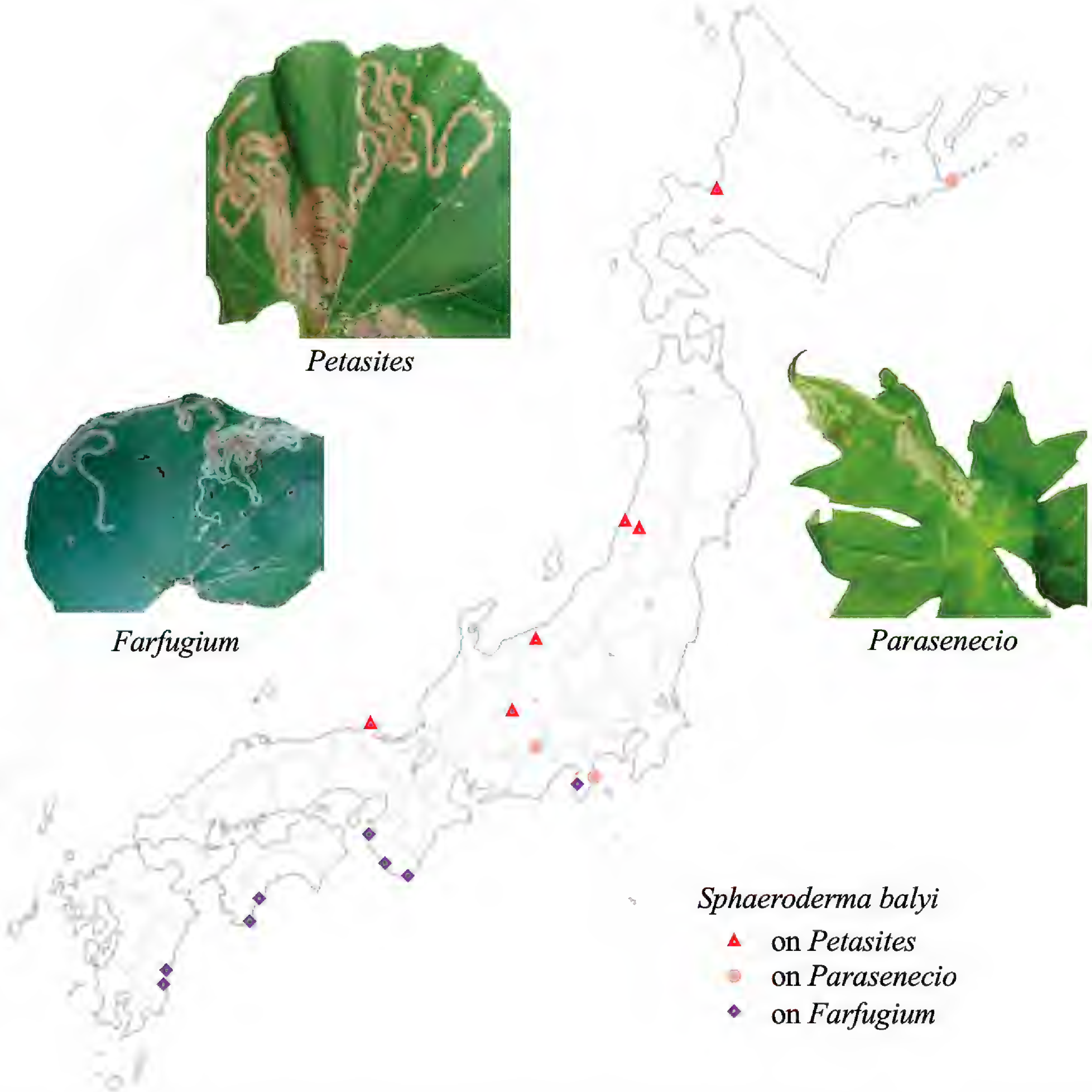

Figure 23. Map showing collection sites of *Sphaeroderma balyi* in the Japanese Archipelago with each recorded host plant genus (*Petasites*, *Parasenecio* and *Farfugium*) indicated by different symbols.

Among the nine *Psylliodes* species in Japan, three (*P. punctifrons*, *P. subrugosa*, and *Psylliodes sasakii*) are associated with the Brassicaceae (Takizawa 2005, 2015), and at least two are confirmed to be leaf miners.

Similar to *Psylliodes*, *Phyllotreta* is also associated with Brassicaceae and comprises leaf-mining, stem-boring, and root-boring species (de Jong et al. 2009; Ellis 2020). There are five *Phyllotreta* species in Japan, and their identification is difficult due to the polymorphism of elytral patterns (Takizawa 2007). Our rearing records suggest that at least two *Phyllotreta* species have leaf-mining habits (Fig. 3A–M), and *P. ezoensis* exhibits elytral polymorphism (Fig. 3A, B).

Evolution of leaf-mining habits

In Chrysomeloidea, cerambycid and megalopodid larvae are respectively wood borers and leaf-miners, while chrysomelid larvae live external or internal life on plants. Our results revealed that there are at least three leaf-mining clades in

Japanese Chrysomelidae: a part of the tribe Alticini in Galerucinae (10 genera), and all members of the tribe Hispini (7 genera) and the tribe Notosacanthini (1 genus) both in Cassidinae (Table 1). Because phylogenetic tree of Chrysomeloidean families is (Chrysomelidae (Megalopodidae, Cerambycidae)) (Cai et al. 2022), and because extant basal clades of Chrysomelidae are external feeders (Nie et al. 2020), leaf-mining life in Chrysomelidae is thought to have evolved from external life in several clades in Alticini and at the base of the two tribes Hispini and Notosacanthini. Further phylogenetic study on Alticini will reveal history of evolutionary shifts between internal and external life in Chrysomelidae.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: MK. Data curation: MK. Funding acquisition: YI. Investigation: MK, YI. Writing - original draft: MK. Writing - review and editing: YI.

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Data availability

All of the data that support the findings of this study are available in the main text.

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